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BEHAVIORAL CHANGES FOLLOWING ABLATION OF THE SUPERIOR COLLICULUS IN THE TREE SHREW

(*TUPAIA GLIS*)

by

Vivien Alice Casagrande

Department of Psychology
Duke University

Date: ______________________

Approved:

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Irving T. Diamond, Supervisor

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Dissertation submitted in partial fulfillment of
the requirements for the degree of Doctor
of Philosophy in the Department of
Psychology in the Graduate School
of Duke University

1973

ABSTRACT

(Psychology-Physiological)

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ABSTRACT

BEHAVIORAL CHANGES FOLLOWING ABLATION OF THE SUPERIOR COLLICULUS IN THE TREE SHREW (*TUPAIA GLIS*)

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Recent studies of the tree shrew have shown that this animal exhibits good visuo-motor coordination and can perform color and simple pattern discriminations after removal of striate cortex. It has been suggested that this visual capacity is maintained by extrastriate visual cortex which receives information indirectly from the superior colliculus via the pulvinar nucleus of the thalamus. When both the extrastriate and striate visual areas were removed, tree shrews did show enormous deficits in simple pattern discrimination although, even with these large cortical removals, the animals exhibited normal visual behavior in their home cages and could discriminate colors (Snyder & Diamond, 1968; Snyder et al., 1969). Presumably the large superior colliculi of these animals contributed to the maintenance of this visual behavior.

In order to gain a better understanding of the role of the superior

colliculus, tree shrews were tested before and after ablation of this area on a series of visual guidance and discrimination tasks. In the first experiment, eight animals were tested for their ability to orient visually and to perform a series of two-choice visual discriminations. In a second experiment, tree shrews were tested for their ability to track and localize visual, auditory, and somatosensory stimuli and for their ability to run through doorways in a set of serially arranged barriers.

The behavioral observations of Experiment I showed that the effect of the lesion of the superior colliculus was dependent upon the depth of that lesion. Those animals with superficial lesions appeared normal on tests of visual guidance, while those animals with deeper lesions appeared blind or grossly impaired. However, both superficial and deep lesions produced similar deficits in visual discrimination. All of the animals, regardless of the lesion, failed to discriminate an upright from an inverted triangle, a large from a small disk, and exhibited difficulty with certain color discriminations. All eight animals succeeded in discriminating black from white and horizontal from vertical stripes. Experiment II added further details concerning the nature of the deficit following the larger lesions. First, it was found that, if a lesion spared a portion of the colliculus, the animal could orient to and follow stimuli in that part of the field which would be represented on the spared portion of the colliculus. Second, it was found that animals with very extensive lesions were also poor at locating auditory and somatosensory stimuli,

although they could localize prolonged painful stimuli. Finally, it was shown that animals even with very large lesions could run through and around a set of barriers better than would have been predicted by their scores in the perimetry tests, suggesting that, in certain circumstances, these animals did have the capacity to guide visually.

Based on the two syndromes produced by superficial and deeper lesions, it is argued that the superior colliculus of the tree shrew consists of two functional subdivisions. It is proposed that the upper division is involved in visual perception, while the lower division is mainly responsible for organizing appropriate movements of the head and eyes in locating and tracking objects.

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INTRODUCTION

Until recently study of the central mechanism of vision in mammals has been concerned chiefly with the visual cortex and its thalamic relay nucleus, the lateral geniculate body. Only in the last decade has there been any concerted effort to gain an understanding of the anatomy, physiology, and function of the superior colliculus which, from the phylogenetic point of view, is the oldest visual center. This is not surprising, since the primary visual area of cortex, area 17, is extremely well developed and is, in fact, the most differentiated part of neocortex in higher primates (Sanides, 1970). Furthermore, clinical evidence certainly tends to support the view that primary visual cortex is essential for any type of vision, since damage to it results in well-defined scotomas (Peele, 1961). Consequently, the superior colliculus was relegated to the secondary role of reflex coordination of eye movements. Over the past decade, however, there have been a number of studies which have clearly demonstrated that removal of area 17 in several different mammals leaves preserved some capacity to perceive and localize objects and patterns (see Doty, 1971). As a result, a number of investigators have turned their attention to other parts of the visual system. In

particular, there has been intense interest in the role of the superior colliculus, particularly since this structure has traditionally been assumed to be essential for vision in all nonmammalian vertebrates and is a major target of the optic tract in mammals and nonmammals alike.

Among mammals, the superior colliculus of the tree shrew is larger than those found in most other mammals. This prominent and well-differentiated structure receives over 80% of the input from the eye (Tigges, 1966). This may explain the fact that removal of area 17 does not have any marked effect on visually guided behavior: for example, simple pattern and color vision remain preserved (Killackey, Snyder, & Diamond, 1971; Snyder, Killackey, & Diamond, 1969). For these reasons, the tree shrew would appear to be the ideal mammal with which to begin investigations of the role of the superior colliculus.

The present results will show that removal of the superior colliculus in the tree shrew has a profound effect on its visually guided behavior and, further, that this effect varies as a function of the depth of the lesion. This finding was considered of sufficient interest to present in preliminary form as a report in Science (Casagrande, Harting, Hall, Diamond, & Martin, 1972).

EXPERIMENT I: VISUAL DISCRIMINATION LEARNING

Method

The design of the experiment described below was to a large extent dictated by difficulties which were encountered in ablating the superior colliculus. Access to the superior colliculus in the tree shrew is particularly difficult since it lies just ventral to the striate cortex and in front of the cerebellum, which is itself connected by the transverse sinus to the cortex. After a number of fully trained adult tree shrews either failed to survive surgery or were rendered untestable through excessive damage to the cerebellum, it was decided that some other approach would be necessary. In the infant tree shrew the superior colliculus is easily accessible since it is not yet covered by the occipital cortex. Ablation of the superior colliculus in the infant animal, as expected, proved to be quite a bit easier. Thus the majority of animals included in this study underwent surgery as neonates. Eventually, collicular lesions were also accomplished in three adult animals with the help of Dr. Ford Ebner. These animals had already received preoperative training one year prior to surgery. Naturally, when the lesion was performed during the neonatal period there was no preoperative training.

The main results of the experiment to be described rests on eight tree shrews, five of which underwent surgery on day 3 after birth and three of which underwent surgery as adults. Six additional subjects were added for behavioral comparison with the main group of eight animals: three of these underwent removal of the striate cortex when they were 3 days old and three of the six were normal.

With two exceptions, all of the animals used in the study were hand-reared from birth and weaned at 1 month to a diet of fruit, cat chow, and water. Hand-reared tree shrews, unlike their wild counterparts, are tractable and friendly, and thus adapt quickly to most testing situations. Two of the subjects (211, 215) were wild and arrived in the laboratory as young adults. These animals required considerable taming before testing began; and one (211) remained rather timid throughout the experiment.

Observations of visually guided behavior

Some of the most useful results showing differences between the three normal animals and the eight cases with superior colliculus lesions were obtained by observing visually guided behavior in the animal's home cage and by using certain tests of their capacity to follow and localize objects and avoid obstacles, etc. The first test was given when the animals were about 6 weeks old, and was designed to assess the animal's capacity to avoid obstacles and notice gaps or "holes" in the floor. The animals were placed in a 3 x 5 x 1-ft. high open wooden arena lined with

eight equal-sized white styrofoam blocks. These blocks could be removed and reorganized in order to create either "gaps" in the floor of the arena or obstacles of various heights, sizes, and shapes. Initially, a young tree shrew was placed at one end of the arena in which a gap was then created in the floor by removing two adjacent blocks. The animal was then enticed to run across the arena and the accuracy of his estimate of the position of the gap and his ability to jump across recorded. The blocks were then rearranged to produce either gaps in other positions or obstacles in the path of the animal. Later several objects (blocks of wood, pieces of metal or plastic, etc.) were placed in the arena. All attempts to explore and navigate in each of these situations were recorded. After the first test each animal was set free on the floor of the laboratory room. Even quite timid tree shrews will move rapidly in such a "free situation" and, consequently, are easier to test. The third test was conducted when the animals matured, which is at about 6 months of age. At this time they were individually observed while freely exploring in the laboratory room for half an hour. During this period the animal was at times encouraged to run and to jump from tables, chairs, or cages on which he was placed in order to get a good estimate of his ability to judge distance.

The preceding tests applied only to those animals which were designated as subjects of the experiment from the time of birth. For those animals that were selected from the adult population, a different

test sequence had to be employed. These animals were observed and tested daily for 2 weeks immediately after surgery in their home cages. During this period observations were made of the animal's ability to orient to and reach out for a food reward (a wax worm held on the end of a pair of forceps) presented in various parts of the visual field. At this time, any changes in body posture and motor coordination were also noted. Following this period, the animals were observed at frequent intervals, up to the time of sacrifice, to determine any changes in visual guidance or motor coordination.

Discrimination training

All eight animals were trained on a series of two-choice discriminations in a Yerkes-type testing box. This apparatus, described previously in detail (see Killackey, Snyder, & Diamond, 1971), consisted of a starting compartment, a choice area, and a stimulus panel containing two hinged doors. Food cups were located behind each door. Either door could be locked by a sliding bolt. Each 4-in. x 4-in. stimulus card (cut from construction paper and sandwiched between pieces of glass) could be mounted in a slide holder behind each door. Light from two Leitz projectors containing 150-watt bulbs transilluminated the stimuli from behind the doors. The apparatus itself was placed in a sound-insulated dark room.

Prior to formal testing, each animal learned first to enter a small

Plexiglas box which was used to transport it from the home cage to the testing chamber. In the apparatus the animal was given several days of adaptation and pretraining. During this period the animal was first allowed to explore the apparatus. Next it was trained to push open either door (plain white stimuli were mounted on both doors) to gain access to a wax worm reward and then to return to the start compartment. Formal training was begun only after the animals opened doors and returned to the starting box without hesitation.

For each of the discriminations (described individually below) the animals were given 10 trials daily. The positions of the negative and positive stimuli were randomized according to a Gellerman (1933) sequence. Each trial began with the animal in the starting compartment and terminated when the animal either pushed the positive or negative door. Following an incorrect response, the stimuli remained in the same position for the following trial. These additional trials were found necessary in order to break position habits. They were recorded but not counted as part of the daily score. Each discrimination was considered learned when the animal had achieved a criterion performance of 19 correct choices in 20 consecutive trials, trials being counted using the procedure just described. All animals were first trained to discriminate between a black and a white card, white being the positive stimulus. Both stimuli were cut from pieces of construction paper. Following criterion performance on the black versus white discrimination, the animals

were trained first to discriminate horizontal from vertical black and white stripes (horizontal positive) and second to discriminate upright from inverted equilateral triangles (upright positive). The stripes, 5/16 in. in width, were made from strips of black tape and white construction paper. The triangles stimuli (1 1/2 in. on an edge) were made of white construction paper and were displayed against the background of black construction paper.

Finally, each animal received postoperative training on several color discrimination tasks. Three animals with lesions of striate cortex were also included in this phase of the experiment.[1] For these discriminations two 4-in. x 4-in. white cards were inserted behind the doors in the same testing apparatus as described above. Two Bausch and Lomb slide projectors with tungsten filament bulbs (Sylvania 150-watt BEH bulbs) transilluminated the cards. Wavelength was varied by Baird Atomic interference filters and intensity was varied by Kodak neutral density filters. The spectral characteristics of the interference filters have been described in an earlier report (Snyder, Killackey, & Diamond, 1969). All of the animals were first trained to choose a green stimulus (570 nm filter) when it was paired with an achromatic stimulus (a white card attenuated with a 1.0 log unit neutral density filter). After the animals had achieved criterion performance on this problem or had

---

[1] An earlier investigation showed that tree shrews without striate cortex could easily make discriminations based on wavelength (Snyder et al., 1969).

20 days of training (whichever came first), they were trained to choose an orange stimulus (610 nm) when paired with the same achromatic stimulus.[1] The tree shrews were given an additional 20 sessions to solve this task. If they achieved criterion within this period, they were then trained on the same task for 30 more sessions, only now the intensity of both the chromatic and achromatic stimuli were randomly varied. The orange (610 nm) stimulus was attenuated with 0.0, 1.0, and 2.0 log unit neutral density filters, while the achromatic stimulus was attenuated with 0.0, 1.5, 3.0, and 4.0 log unit neutral density filters. Following this task the 610 nm (orange) stimulus was paired with a 450 nm (blue) stimulus with 610 nm positive. The 610 nm stimulus was attenuated with a 0.6 log unit neutral density filter and thus appeared (to the human observer) to be roughly equivalent in brightness to the 450 nm stimulus.[2] If and when criterion performance was achieved on this problem, the animals were given the same task as a final discrimination with intensity randomly varied. The 610 nm filter was attenuated with 0.0, 0.5, 1.2, and 2.0 log unit neutral density filters, while the 450 nm filter was attenuated with 0.0, 0.5, and 1.0 log unit neutral density filters. In the tasks where intensity was randomized, the animals were always given a

---

[1] Since the tree shrew is a dichromat with a neutral point at about 504 nm, one would expect that if the animal had learned the first discrimination he would then transfer to the second task since both chromatic stimuli were on the same side of the neutral point (Snyder et al., 1969).

[2] According to Tigges, Brooks, and Klee (1967), the photopic visibility function of normal tree shrews is similar to that of man.

different combination of intensities for every trial. When the animal achieved criterion performance (19 correct responses in 20 trials) it was given an additional 8 days' training to determine if it had committed errors only with certain intensity combinations. The details of this particular procedure have been described in an earlier report (see Snyder et al., 1969).

An additional problem was given just to the three animals which underwent surgery as adults. In this task the animals were required to discriminate a large from a small white disk displayed on a black background (large positive). The large disk (25 square centimeters) was twice the area of the smaller one (12.5 square centimeters). Flux and brightness cues were eliminated by placing a 0.3 Kodak neutral density filter (50% transmittance) behind either of the stimuli in a random sequence. When criterion performance had been achieved the animals were given a series of generalization tests to determine if they had been responding to the relative or the absolute size of the disks. During these tests the positive stimulus was paired with one twice its size and the negative stimulus with one half its size. Each test trial (with one of the above combinations) was always given following two correct responses to the original pair of training stimuli. The animal was rewarded for either choice during a test trial. A total of 20 test trials on each combination was presented to each animal.

Surgical procedures

The description of surgical procedures will be considered in two parts since slightly different methods were employed in producing lesions in neonatal as compared with adult animals. All but three of the animals in this study underwent surgery on day 3 after birth. In the three animals (211, 215, and 223) which underwent surgery as adults, approximately one year had elapsed following the completion of preoperative training.

Adults. For several days prior to surgery each animal received a vitamin K supplement (mephyton) in his daily diet in order to promote rapid blood clotting. Before surgery began the animal was weighed and given atropine to control salivation, and Sparine as a muscle relaxant. One-half hour later deep anesthesia was achieved by an interperitoneal injection of sodium pentobarbital.

During surgery the animal's head was secured in a stereotaxic headholder. Using a dental drill, a large section of bone was removed (in one piece) in order to expose both the occipital lobe and cerebellum. The bone itself was kept in a beaker of cold sterile saline and later replaced. To gain access to the superior colliculi, the dura was incised behind the transverse sinus and pulled back toward the cerebellum. Using dental instruments, modified for the purpose, the cerebellum was retracted and the cortex elevated slightly until the posterior parts of the colliculi could be visualized with the aid of a Zeiss Techniscope. The

superior colliculi were then removed bilaterally with gentle aspiration using a glass pipette. Any bleeding which occurred during surgery was controlled with Gelfoam or Surgicel. Following the ablation the bone was replaced and secured with dental cement and the overlying tissue sutured. Aseptic precautions were maintained throughout the surgical procedure. After surgery all animals received 30, 000 units of penicillin to guard against infection.

Infants. The surgery in infant tree shrews was in all cases done on day 3 after birth. Prior to surgery the infants were routinely given atropine to prevent respiratory congestion. During surgery they were continually given small doses of ether to maintain a light level of anesthesia. To gain access to the superior colliculi or striate cortex, depending on the case, the overlying bone was removed. On day 3 after birth the visual cortex has not yet covered the superior colliculi, making surgical removal of these structures far simpler than in the adults. All lesions were made by aspiration. Following surgery the animals were administered 3, 000 units of penicillin to prevent infection.

Histological procedures

After the animals had completed the behavioral tasks they were perfused with saline and 10% formalin. The brains were removed and sectioned in the frontal plane. Five of the animals (215, 223, 299, 300, 303) underwent a removal of one eye 3 to 5 days prior to sacrifice. In

these cases at least every tenth section (cut at 30 microns) was processed by the Fink-Heimer (1967) method for tracing degenerating axons and their terminal endings. The main reason for this was to determine if there had been any changes in the normal distribution of retinal fibers as a result of the midbrain or cortical ablations.[1] Adjacent sections were stained either for Nissl bodies or myelin in order to give a picture of the cell and fiber detail. In the remaining cases, sections were stained for Nissl substance only. The extent of the lesion of the superior colliculi was estimated by comparison with sections from the same levels in normal material. Representative sections were then selected and photographed. In the three cases with lesions of the striate cortex, careful analysis of retrograde changes in the thalamus were made. Sections from these brains were chosen to illustrate these changes and are presented in Results.

Results

Observations of visually guided behavior

The main result was apparent almost immediately following surgery from observations of the animals in their home cages. Two of the eight animals (299 and 300) appeared completely normal, while the remaining six looked surprisingly blind, remaining impassive even when threatening

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[1] Schneider (1970) has been able to demonstrate changes in the retino-fugal fiber pattern following neonatal superior colliculus lesions in hamsters.

gestures were made close to their faces.

The two animals (299, 300) which appeared normal in their home cage were also normal on all tests of motor coordination, obstacle avoidance, and visual orientation as described in Methods. The remaining six animals differed with respect to their deficits on these tests and therefore will be considered individually below.

Three of the six animals (327, 328, and 329) underwent surgery on day 3 after birth and were tested between 5 and 7 weeks later. When tested at this time none of these animals was able to orient to or follow a moving tidbit of food or to avoid capture when placed on the floor of the experimental room, often running toward rather than away from the experimenter. Two of the latter group (327, 329) exhibited difficulties in motor coordination and often went into fits of circling. Tupaia 327 also exhibited spontaneous nystagmus, bumped into objects and fell into gaps in its path, although in the same situation Tupaia 328 and 329 appeared to be able to avoid obstacles well and to jump across a hole placed in their path. All three animals tended not to turn their heads as much as a normal tree shrew while moving about, which gave them a stiff appearance. However, they did appear to have normal control of their neck muscles in other situations since they had no difficulty grooming themselves. All of these behavioral peculiarities remained unchanged as the animals were tested and retested as adults up to the time of their sacrifice one and a half years later.

The remaining three animals (211, 215, 223) underwent surgery as adults. On the first postoperative day they appeared blind and exhibited various motor difficulties. Tupaia 215 seemed to have the worst motor problem and often lost its balance while attempting to move. Unlike the animals who underwent surgery as neonates; these animals recovered from their motor problems and appeared well coordinated at the end of the second postoperative week.[1] However, they continued to appear "stiff necked" while in motion and remained poor in tests of visual orientation and following. Also, when placed on the floor of the experimental room, they ran forward, avoiding obstacles in their path, but appeared unaware of the approach of anyone in the room and thus never took evasive action. By the end of the second postoperative week two of the animals (211, 215) still showed no sign of being able to follow a moving target, although the third animal (223) was now able to track an object moving very slowly while always keeping its head held forward and downward. At this time both Tupaia 223 and 215 were able to reach out for some stationary food tidbits placed directly in front of them, although they were still unresponsive to visual threat. Tupaia 211 never showed any signs of ability to visually follow or orient to stimuli in any part of the field. No further

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[1] The difference between groups of animals was more likely due to the degree of cerebellar damage rather than age at the time of surgery. Tupaia 327, 328, and 329, which were neonates at the time of surgery, were found to have moderate damage to the cerebellum, unlike the three animals (211, 215, 223) which underwent surgery as adults and had no damage to the cerebellum.

improvements in visually guided performance was noted in these three animals even after a year.

Discrimination training

From the observations just described, it appeared that the group of eight animals could be divided into two classes: two animals appeared normal while the remaining six animals appeared blind, or nearly so. Yet, when tested on the formal discrimination tasks, all of the animals performed in a surprisingly uniform manner. After surgery all of the animals learned to discriminate white from black and horizontal from vertical stripes, yet they failed to discriminate an upright from an inverted triangle, disks of different sizes, and exhibited deficits in color discrimination.

Since tree shrews show a normal tendency to choose white over black, it was difficult to assess whether the three animals which received preoperative training actually retained or had to relearn this task, while on the stripe discrimination it was obvious that they did have to relearn the task.

The number of errors committed by all eight animals on the task requiring the discrimination of the orientation of stripes is shown in Figure 1. Learning curves of each of the animals by session are shown in Figures 2-4. After surgery, all but two of the animals learned this discrimination in the same time and with the same number of errors as

Figure 1. Errors to Criterion for Each Animal on the Discrimination of Horizontal from Vertical Stripes.

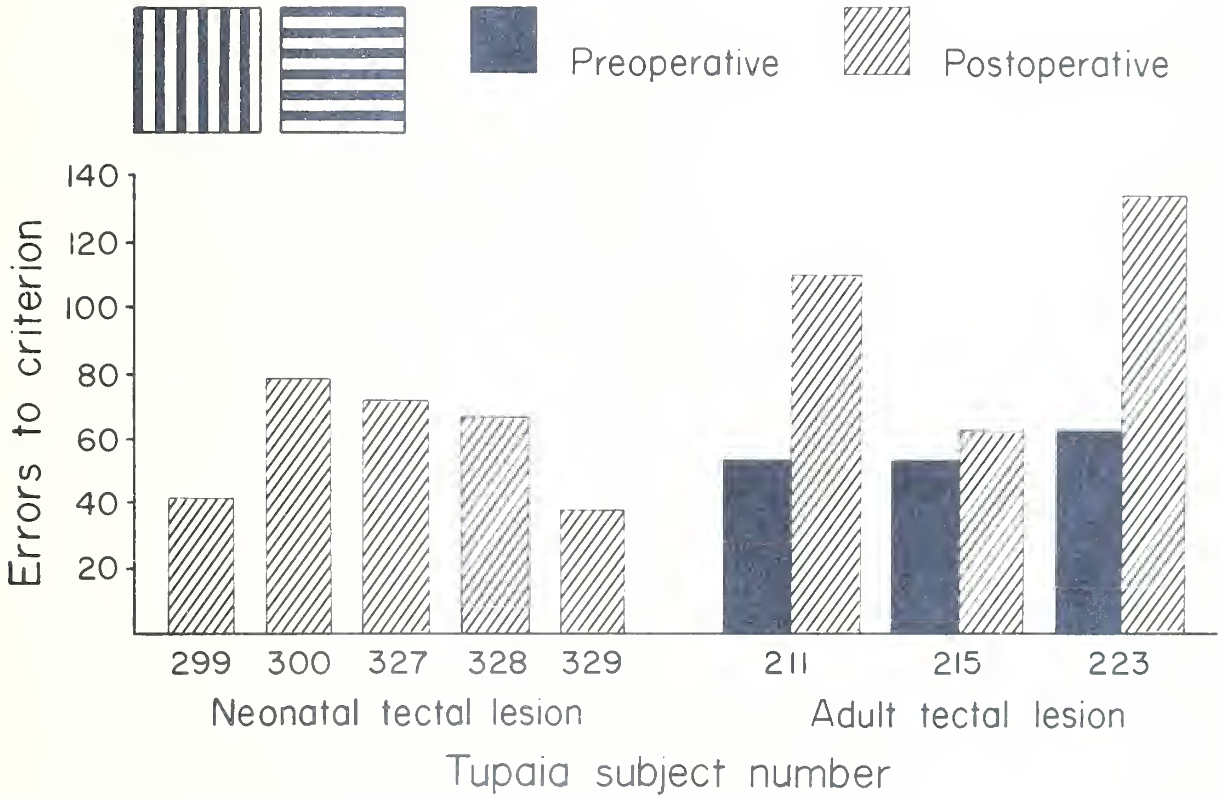
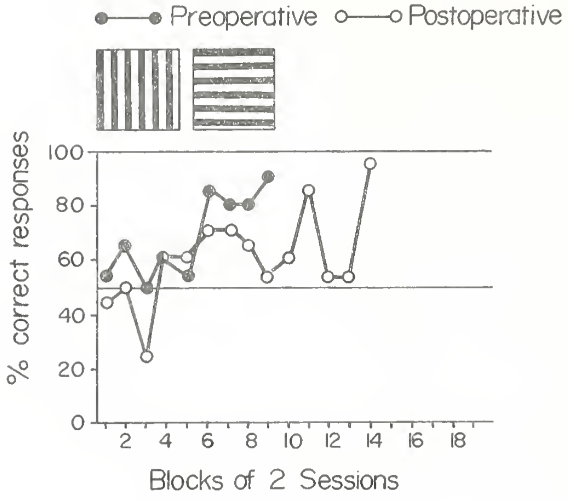
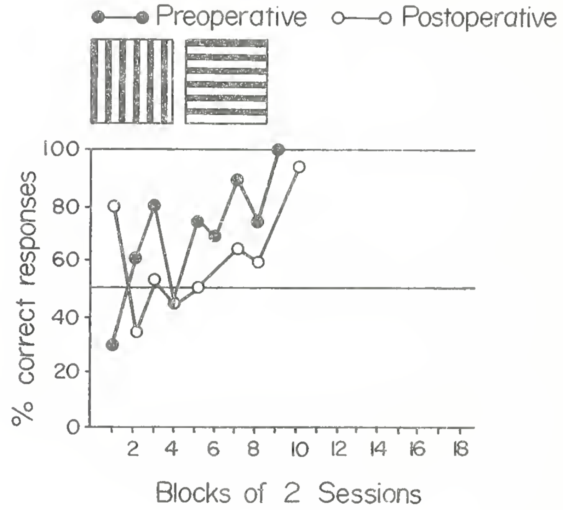

Preoperative
Postoperative
Errors to criterion
140
120
100
80
60
40
20
299
300
327
328
329
211
215
223
Neonatal tectal lesion
Adult tectal lesion
Tupaia subject number

Figure 2. Performance Records of Tupaia 211, 215, and 223 before and after Ablation of the Superior Colliculus.


TUPAIA 211 - Tectal Lesion as Adult


TUPAIA 215 - Tectal Lesion as Adult

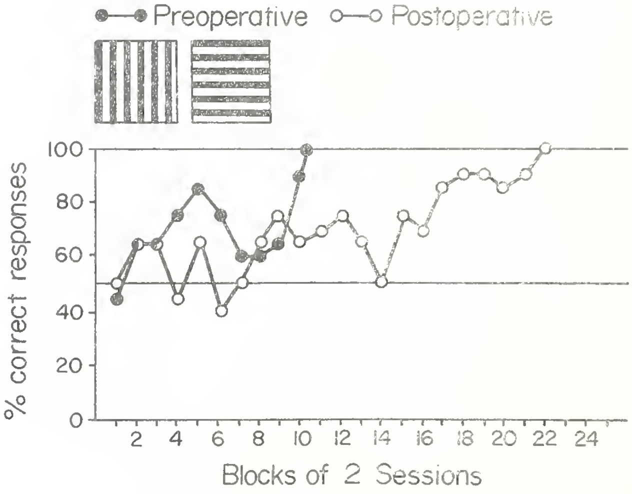
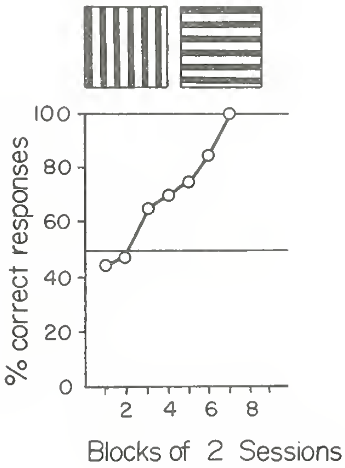

TUPAIA 223 - Tectal Lesion as Adult

Figure 3. Performance Records of Tupaia 299 and 300 after Ablation of the Superior Colliculus.

TUPAIA 299- Tectal Lesion as Neonate



TUPAIA 300- Tectal Lesion as Neonate

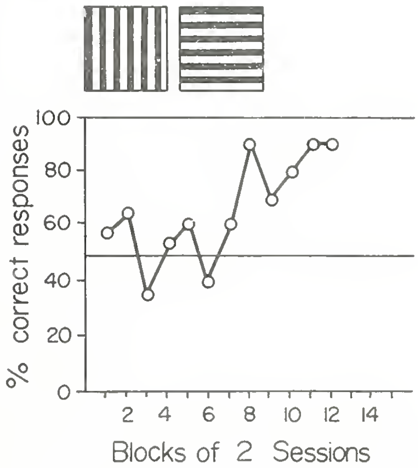
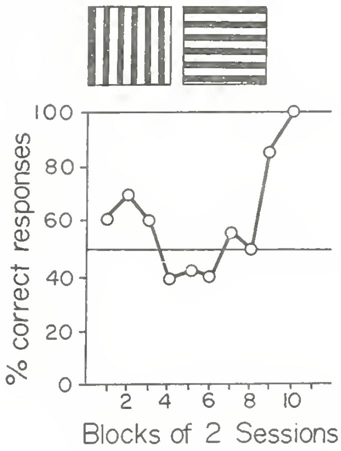
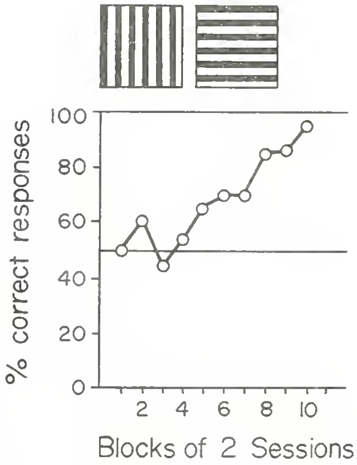


Figure 4. Performance Records of Tupaia 327, 328, and 329 after Ablation of the Superior Colliculus.

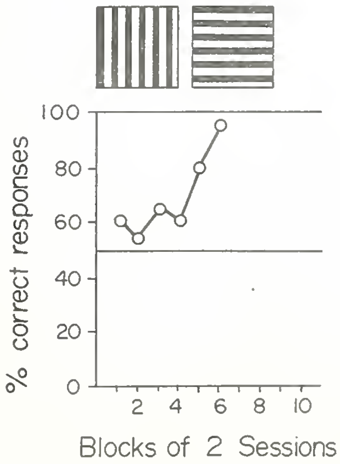
TUPAIA 327 – Tectal Lesion as Neonate



TUPAIA 328 – Tectal Lesion as Neonate



TUPAIA 329 – Tectal Lesion as Neonate

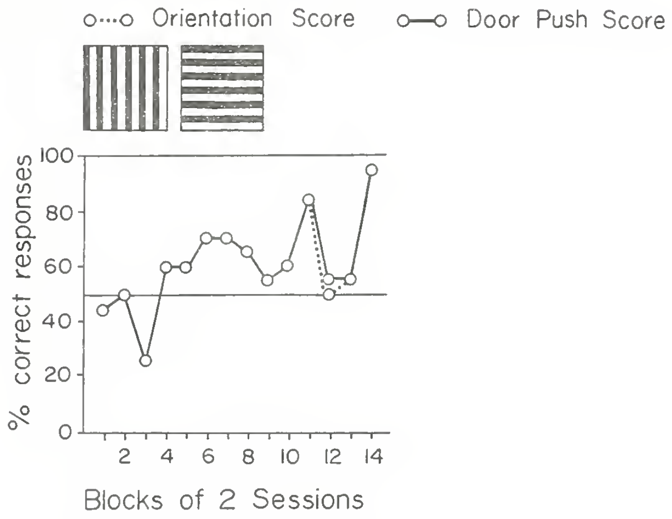


normal animals. Tupaia 211 and 223 took longer to relearn this task and correspondingly made more errors. The difference between these two exceptional animals and the others could not be attributed to differences in their lesions (see histological results) or to a difference in age at the time of surgery.

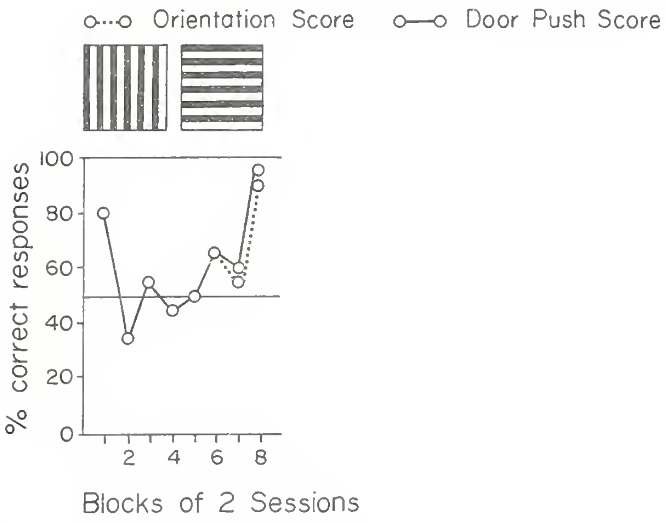
The success of the animals on the stripe discrimination following removal of the superior colliculus is consistent with the results reported by Schneider (1969) in a similar experiment using the hamster. However, Schneider made the claim that if an error was now scored for every approach to the negative door instead of every push of the negative door (as in the present experiment), then his hamsters failed to discriminate. It is reasonable to ask whether a deficit in this task would be revealed if errors were scored the way Schneider did. Therefore, from the beginning records were kept of any approaches (errors of "orientation") to the negative door closer than 4 in., the length of the opaque divider between the doors. Figures 5-7 compare the performance of all of the animals when errors were scored by the second method. Four of the eight animals showed almost no difference in their ability to perform this task when scored by the second method, while the remaining four animals showed some differences in performance when scored this way. In spite of this, only one animal, Tupaia 327, actually remained at chance level when errors of orientation were scored. It should be recalled that this animal had a severe motor handicap, and thus tended to adopt a rather

Figure 5. Performance Records of Tupaia 211, 215, and 223 after Ablation of the Superior Colliculus According to Two Different methods of Scoring Errors. See text for details.

TUPAIA 211 - Tectal Lesion as Adult



TUPAIA 215 - Tectal Lesion as Adult



TUPAIA 223 - Tectal Lesion as Adult

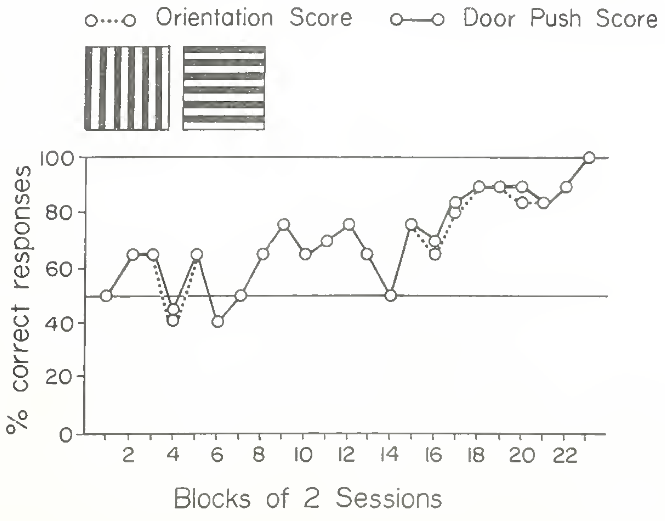
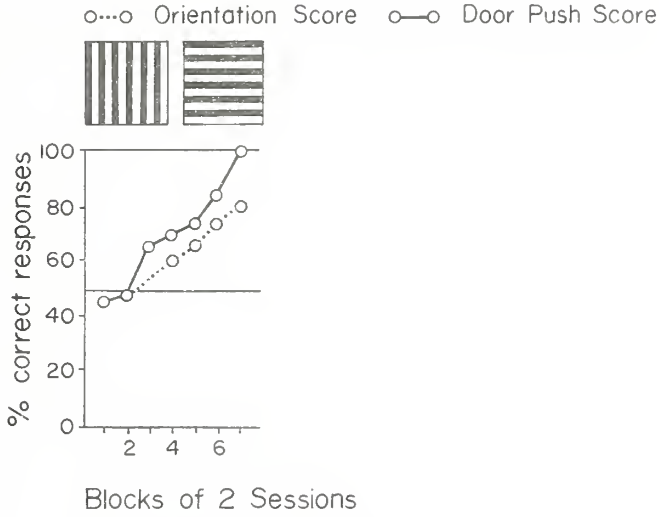


Figure 6. Performance Records of Tupaia 299 and 300 after Ablation of the Superior Colliculus According to Two Different Methods of Scoring Errors. See text for details.


TUPAIA 299 - Tectal Lesion as Adult

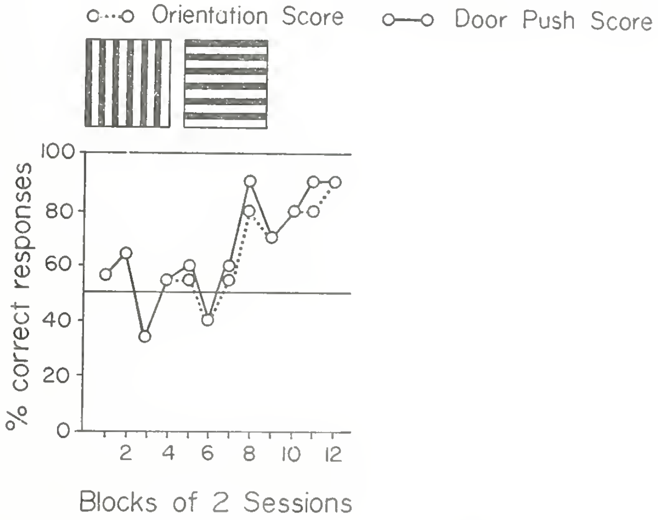
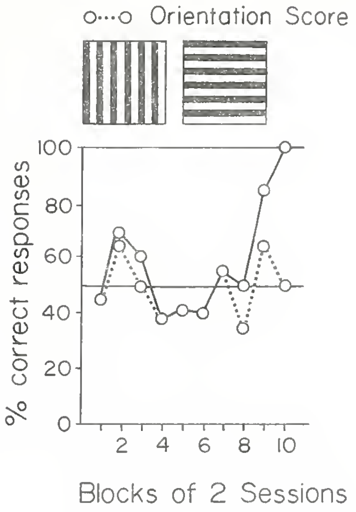
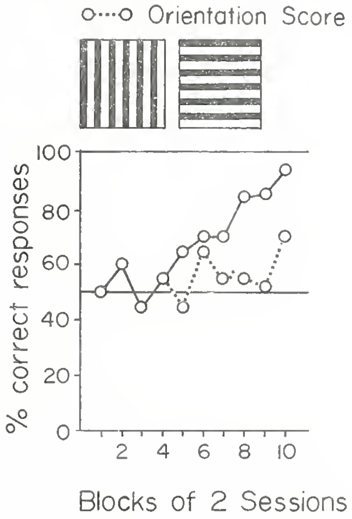

TUPAIA 300 - Tectal Lesion as Neonate

Figure 7. Performance Records of Tupaia 327, 328, and 329 after Ablation of the Superior Colliculus According to Two Different Methods of Scoring Errors. See text for details.

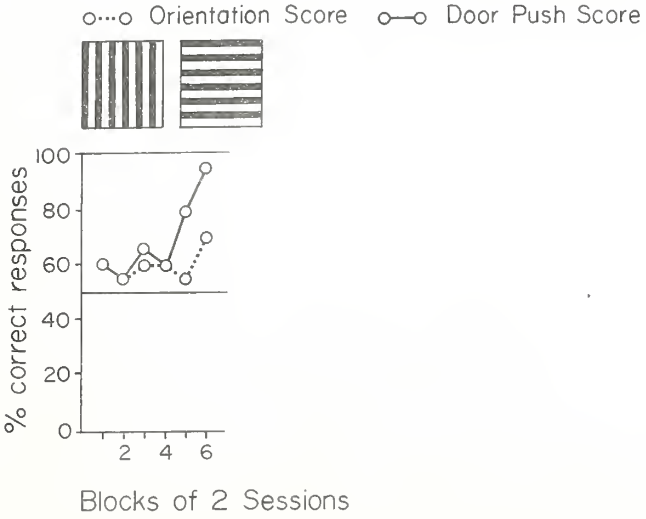
TUPAIA 327 - Tectal Lesion as Neonate



TUPAIA 328 - Tectal Lesion as Neonate



TUPAIA 329 - Tectal Lesion as Neonate



rigid path habit in learning to discriminate. Two other animals (328, 329) also appeared to adopt more rigid path habits, occasionally hugging close to the walls of the apparatus. All of the other animals appeared to adopt normal strategies for solving the task. The difference between the animals was not related to the completeness of the lesion of the superior colliculus (see histological results), although damage to other structures, particularly the cerebellum with its concomitant motor disabilities, might have contributed to lower performance scores.

Following the discrimination of stripes, the tree shrews were trained to discriminate an upright (positive) from an inverted (negative) equilateral triangle. Figure 8 shows the total number of errors committed by each animal, while Figures 9-11 show the learning curves of each animal by session. Postoperatively, none of the animals was able to achieve criterion on the triangle discrimination within 80 sessions.

All of the animals except Tupaia 329[1] were also tested postoperatively on a series of color discrimination problems. Their performance was compared with three animals with neonatal lesions of striate cortex. Table 1 summarizes the performance scores of each of the animals. Representative examples of individual learning curves of four of the animals are shown in Figures 12 and 13. On the first discrimination, 570 nm versus white, all three of the animals with lesions

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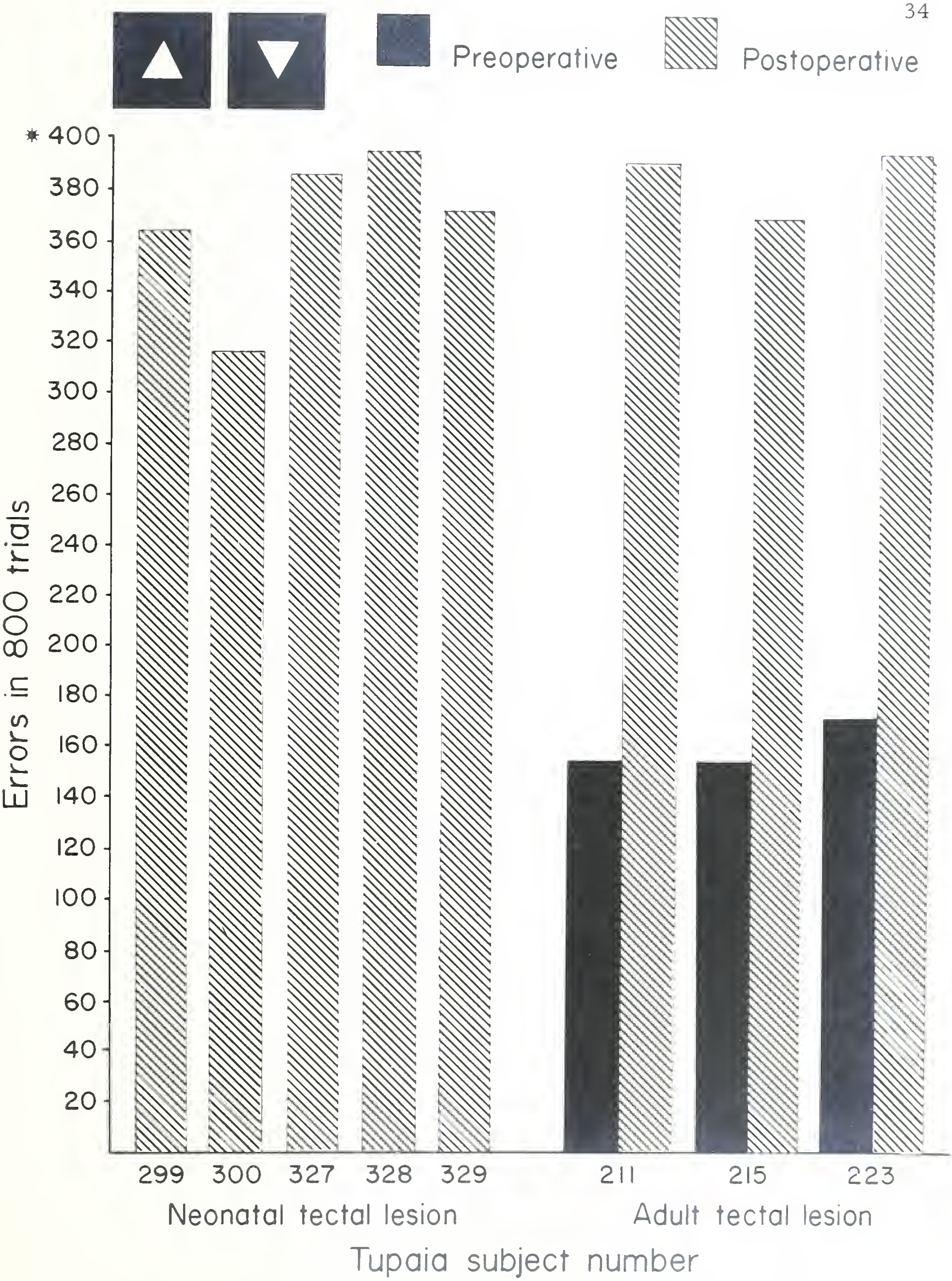
[1] Tupaia 329 died following its training on the triangle discrimination.

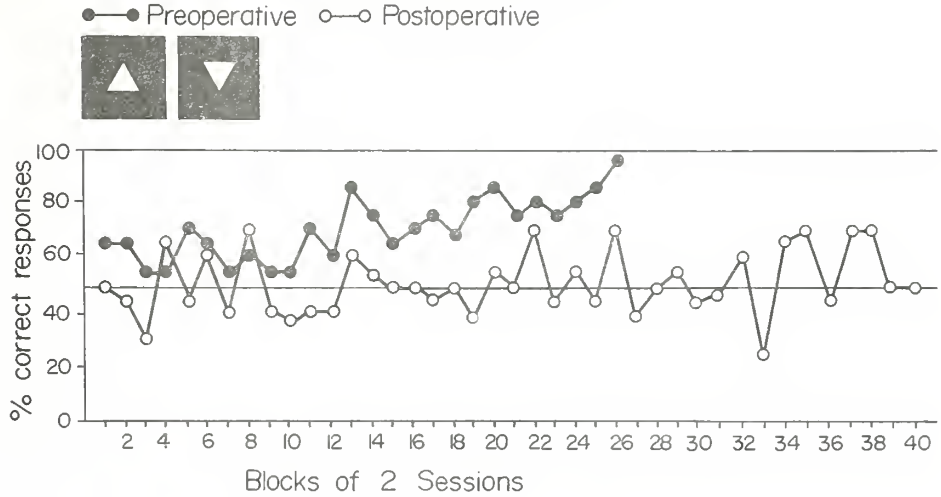
Figure 8. Errors in 800 Trials for Each Animal on the Discrimination of Upright from Inverted Triangles.



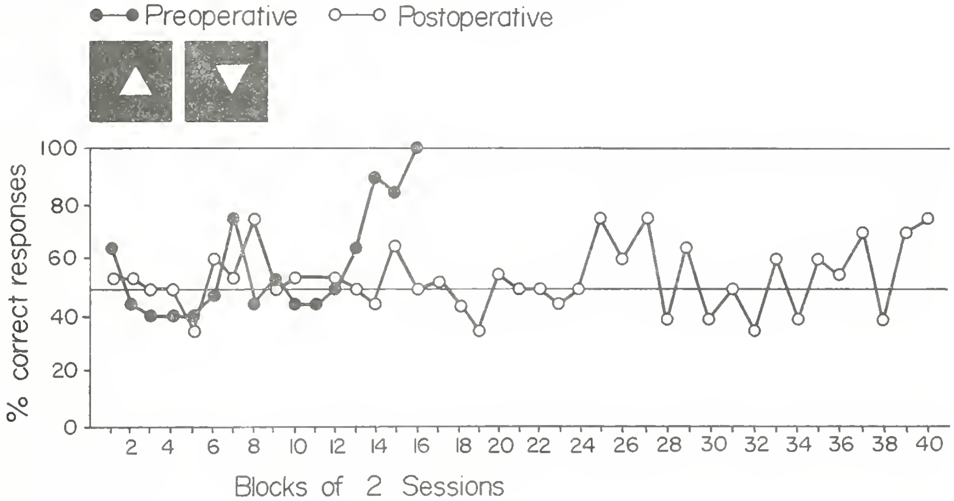
* Chance performance

Figure 9. Performance Records of Tupaia 211, 215, and 223 before and after Ablation of the Superior Colliculus.

TUPAIA 211 - Tectal Lesion as Adult



TUPAIA 215 - Tectal Lesion as Adult



TUPAIA 223 - Tectal Lesion as Adult

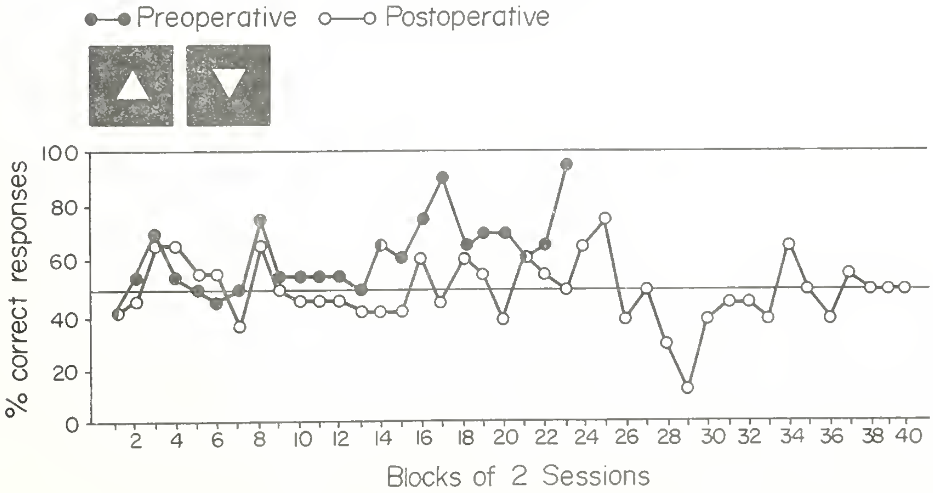
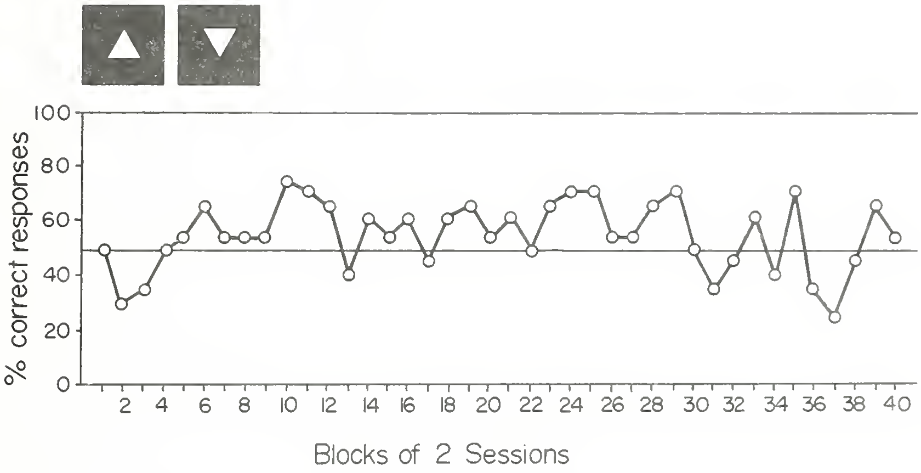


Figure 10. Performance Records of Tupaia 299 and 300 after Ablation of the Superior Colliculus.

TUPAIA 299 – Tectal Lesion as Neonate



TUPAIA 300 – Tectal Lesion as Neonate

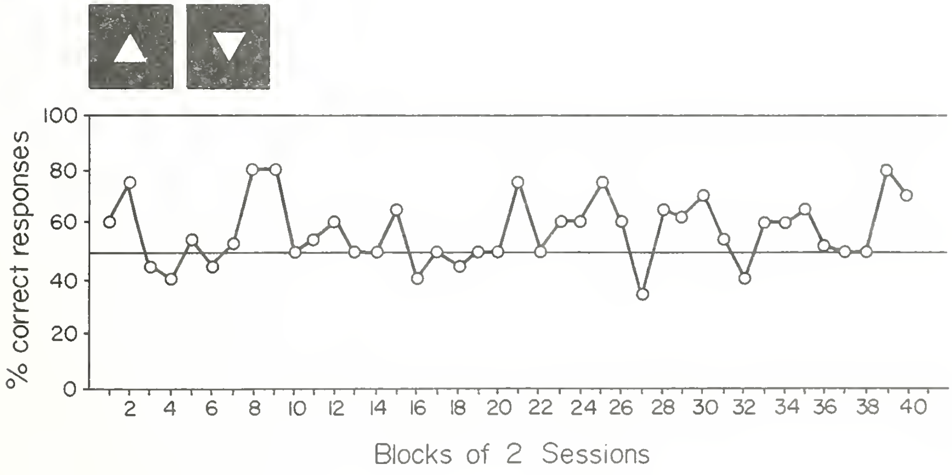
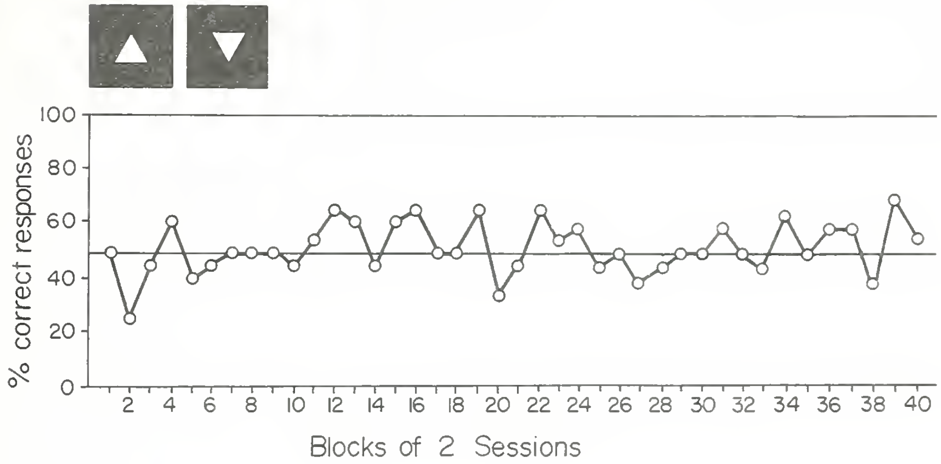
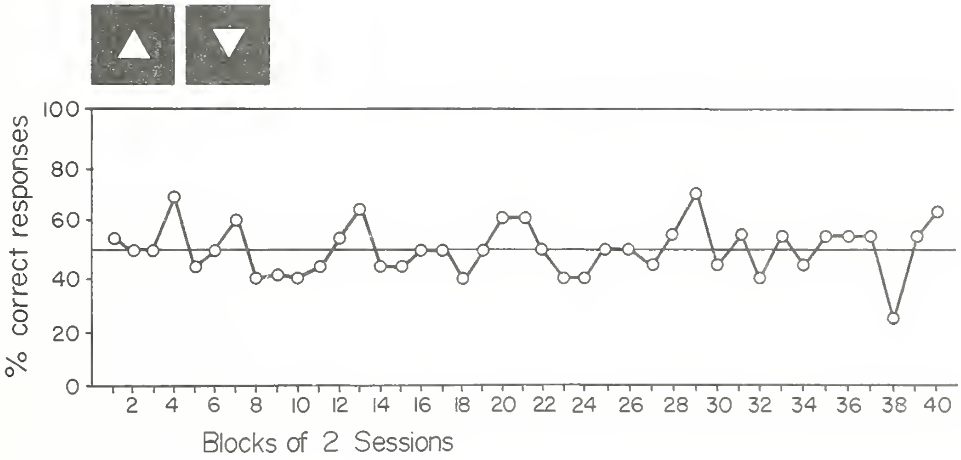


Figure 11. Performance Records of Tupaia 327, 328, and 329 after Ablation of the Superior Colliculus.

TUPAIA 327 – Tectal Lesion as Neonate



TUPAIA 328 – Tectal Lesion as Neonate



TUPAIA 329 – Tectal Lesion as Neonate

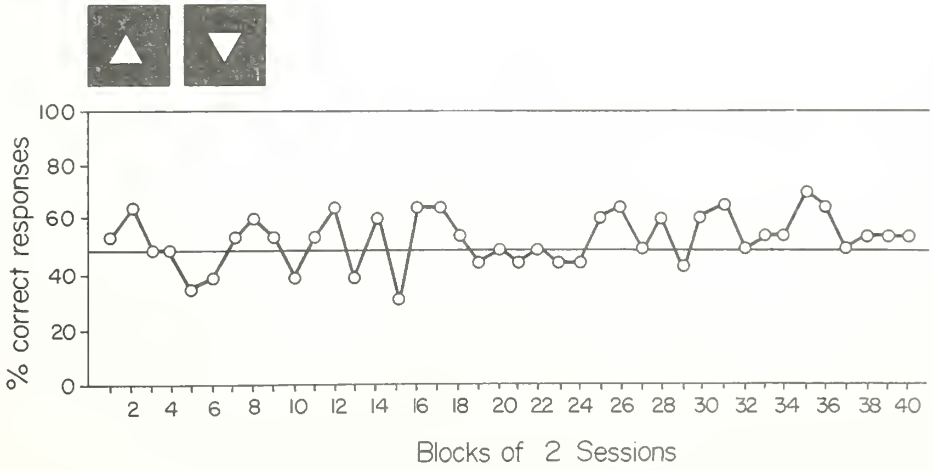


Table 1

Performance Scores on Color Discriminations

Animal	Lesion	Sessions to Criterion				
		570+ White-	610+ White-	610+ White- (Brightness Varied)	610+ 450-	610+ 450- (Brightness Varied)
304	Striate lesion as neonate	7	2	10	2	2
303		23[a]	2	7	2	2
323		10	5	8	3	2
299	Superficial tectal lesion as neonate	F	F		7	4
300		F	20	31[a]	4	2
327	Deep tectal lesion as neonate	F	F	-	F	-
328		F	F	-	21	16
211[b]	Deep tectal lesion as adult	F	F	-	22	-
215		F	F	-	4	9
223		F	F	-	2	16

Note.--F indicates that the animal failed to achieve criterion performance within 20 days each on the first two discriminations (from left to right) and 30 days each on the last three discriminations.

[a] Animals 303 and 300 were allowed to complete the task since their performance was well above chance on the last few sessions.

[b] 211 died before achieving criterion on the final discrimination.

Figure 12. Performance Records of Tupaia 323 on Each Color Task after Removal of Striate Cortex.

TUPAIA 323 - Striate Lesion as Neonate

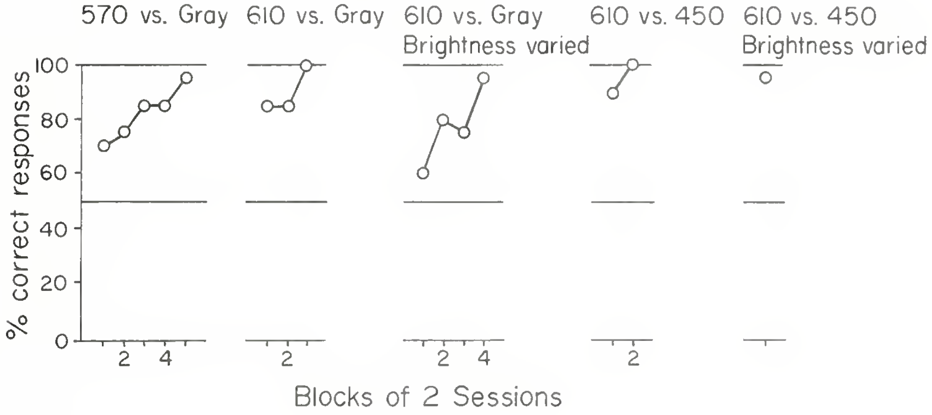
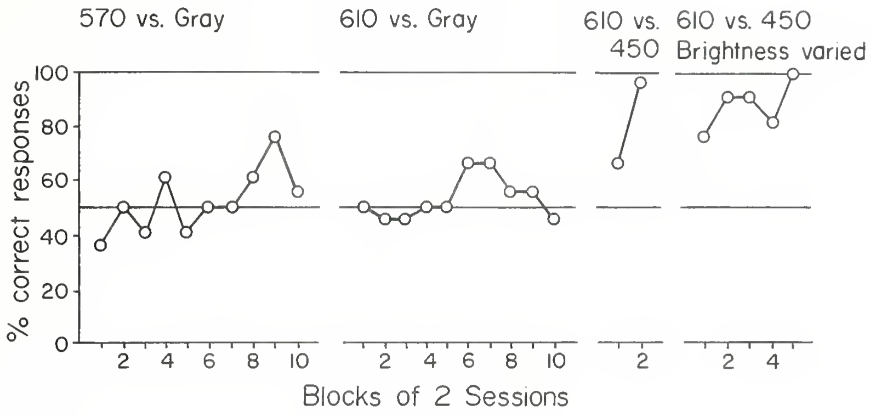
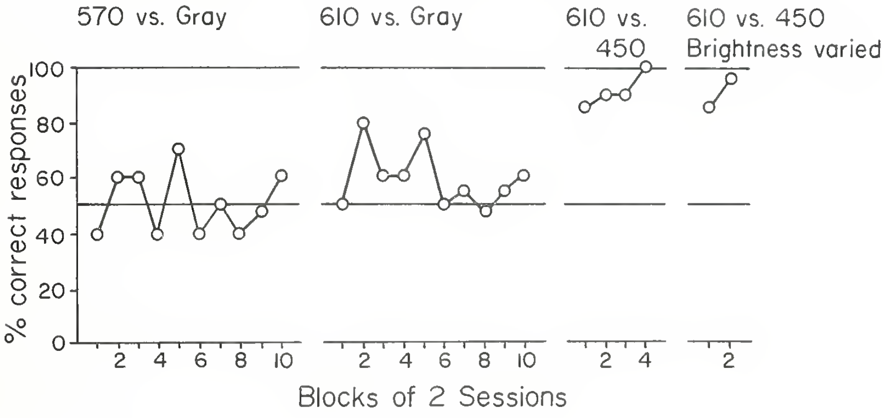


Figure 13. Performance Records of Tupaia 215, 299, and 328 on Each Color Task after Ablation of the Superior Colliculus.

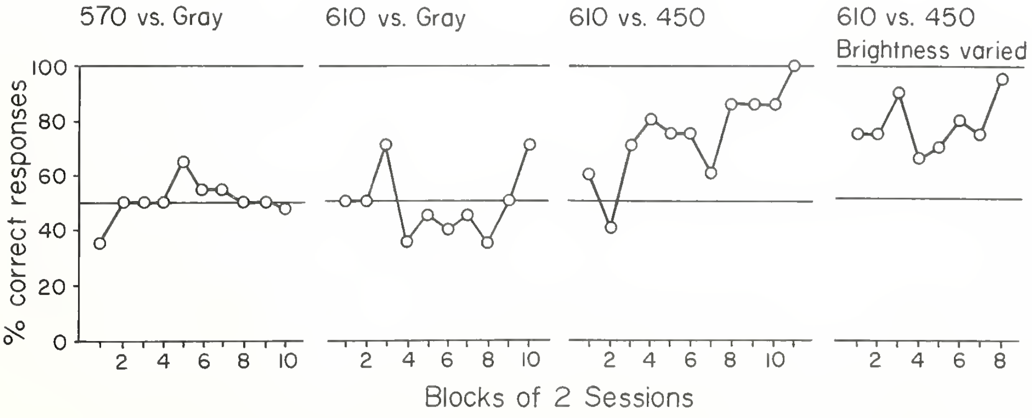
TUPAIA 215 – Tectal Lesion as Adult



TUPAIA 299 – Tectal Lesion as Neonate



TUPAIA 328 – Tectal Lesion as Neonate



of striate cortex were able to achieve criterion performance. Following this training, the animals with striate lesions showed immediate transfer to the second task, 610 nm versus white; two of the three animals made only a single error on this problem. When the intensity of both the 610 nm and the achromatic stimulus covaried in the third task, the animals with striate lesions again transferred at above chance levels and rapidly achieved criterion. In essence, then, the animals with striate lesions had no difficulty with any of these color discriminations. In contrast, all but one of the animals with lesions of the superior colliculus failed to achieve criterion on either of the first two problems. Tupaia 300 was able on the final day to achieve criterion on the second task; however, this animal did not transfer to the third problem where the intensity was covaried, suggesting that the animal may have been attending to intensity rather than to wavelength on the second problem. Tupaia 300 did eventually achieve criterion on this task but only after a much longer period of time than was required by any of the animals with striate lesions. On the fourth color task the animals were required to discriminate 610 nm from 450 nm with intensity held constant. The animals with striate lesions transferred immediately to this task from the previous one and went on to a fifth task in which the intensity was covaried without a drop in performance. All but one (327) of the animals with lesions of the superior colliculus were also able to achieve criterion on both of these tasks, although three of these animals did take longer than

the animals with striate lesions. Both Tupaia 211 and 328 required many more sessions than the others to achieve criterion where intensity was held constant. On the fifth task, where intensity was covaried, Tupaia 223 and Tupaia 328 took longer than the others to achieve criterion. Tupaia 211 died before completing this task but had not achieved criterion by the sixteenth session although at this time performance was at a level well above chance.

From the above it can be concluded that, unlike lesions of the visual cortex, lesions of the superior colliculus interfere with, but do not abolish, the ability to discriminate hues. To some extent, the animal's difficulty appeared to be related to the size of its lesion. Tupaia 300 had the smallest and most superficial lesion of the superior colliculus, and Tupaia 327 had one of the deepest lesions. It is doubtful, however, that the complete failure of Tupaia 327 on all tasks can be attributed to the removal of the superior colliculus alone; three other animals had complete lesions of the superior colliculus and did demonstrate the ability to discriminate 610 nm from 450 nm. The failure of Tupaia 327 could have been the result of emotionality because this animal had great motor difficulties. Each trial required great effort, and failures often caused it to go into uncontrolled fits of circling.

In addition to the color discriminations, the three animals were also trained to discriminate disks of different sizes. Their individual pre- and postoperative performance scores in terms of total number of

errors is shown in Figure 14. Session by session learning curves are presented in Figure 15. Preoperatively, all three of the animals were easily able to achieve criterion performance. Tests of generalization on which the positive and negative stimuli were paired with stimuli twice as large or half as large, respectively, indicated that the animals were performing the tasks on the basis of relative size rather than absolute size of the original stimulus pair. Postoperatively, all three of the animals failed to achieve criterion performance on the task within 40 consecutive training sessions.

In summary, all of the eight animals with lesions of the superior colliculus were similar in their behavior in the formal tests of visual discrimination, but there was a marked difference between two out of the eight animals in tests of visual guidance: two of the animals appeared completely normal, while the remaining six appeared blind, or nearly so. On the tests of visual discrimination the animals were able to distinguish light from dark and to distinguish patterns based on the orientation of stripes, and yet they failed to discriminate an upright from an inverted triangle, disks of different sizes, and exhibited difficulties in color discrimination.

Histological results

Lesions of the superior colliculus.

A tentative explanation for the difference between the two groups was provided by histological analysis

Figure 14. Errors in 400 Trials for Each Animal on the Discrimination of a Large from a Small Disk.

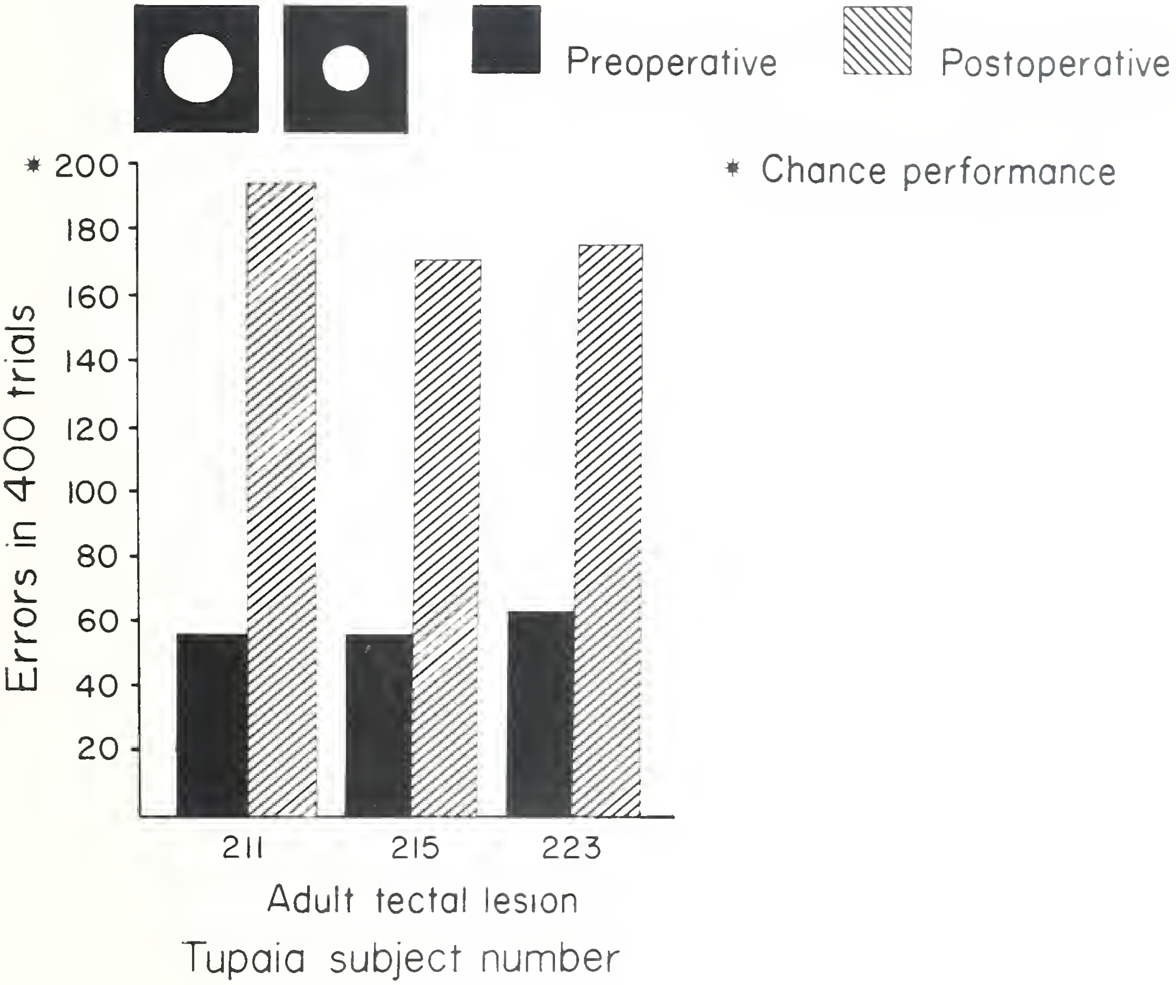
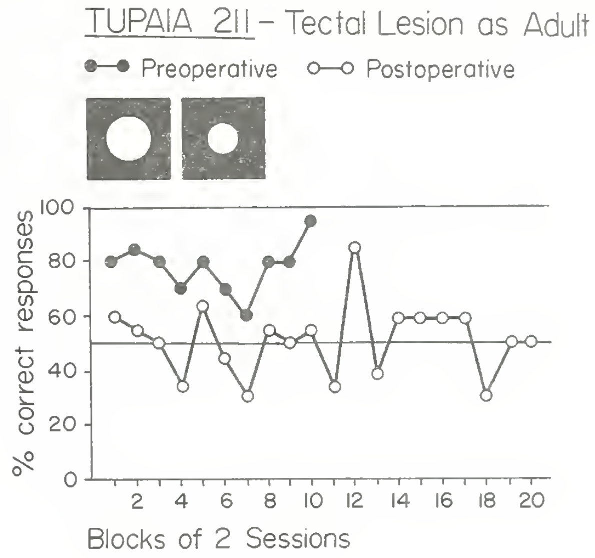
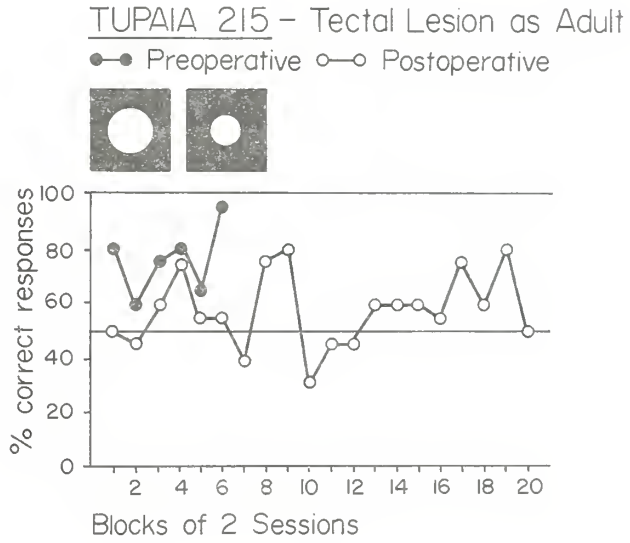
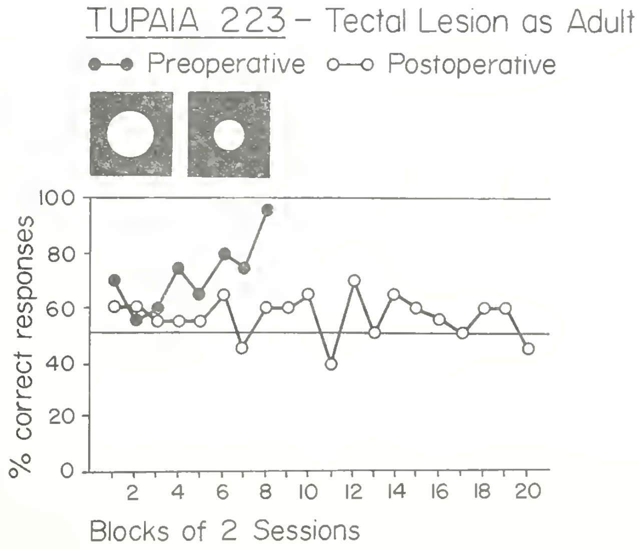

Preoperative
Postoperative
* Chance performance
* 200
180
160
140
120
100
80
60
40
20
Errors in 400 trials
211
215
223
Adult tectal lesion
Tupaia subject number

Figure 15. Performance Records of Tupaia 211, 215, and 223 before and after Ablation of the Superior Colliculus.


TUPAIA 211 – Tectal Lesion as Adult
●—● Preoperative ○—○ Postoperative
% correct responses
0
20
40
60
80
100
2
4
6
8
10
12
14
16
18
20
Blocks of 2 Sessions


TUPAIA 215 – Tectal Lesion as Adult
●—● Preoperative ○—○ Postoperative
% correct responses
0
20
40
60
80
100
2
4
6
8
10
12
14
16
18
20
Blocks of 2 Sessions


TUPAIA 223 – Tectal Lesion as Adult
●—● Preoperative ○—○ Postoperative
% correct responses
0
20
40
60
80
100
2
4
6
8
10
12
14
16
18
20
Blocks of 2 Sessions

of the lesions. The two animals which appeared normal in visually guided behavior had lesions which were restricted mainly to layers 1 and 2 of the superior colliculus. Tupaia 300 received the smaller lesion of the two and the smallest lesion of any animal in the study (see Figure 17).[1] In both cases, all of the pretectum and portions of layers 2 and 3 remained intact. Also, in both cases there was slight damage to the dorsal part of the caudal central grey.

In contrast to Tupaia 299 and 300, the five animals which were completely unable to follow a moving target all had complete or nearly complete lesions of the superior colliculus. Three (327, 328, 329) of the five had very similar lesions which included complete removal of the superior colliculus as well as extensive damage to the pretectum, inferior colliculus, and central grey, and (to a lesser degree) to the tegmentum and caudal extremity of the dorsal thalamus (see Figure 18). In two of these animals (328, 329), the left half of the cerebellum was almost totally removed, while in the third animal (327) the middle and right half of the cerebellum was extensively damaged. Damage to the cerebellum and tegmentum may explain some of the motor difficulties which were seen in these three animals.

Two of the five cases (211, 215) had lesions which were less

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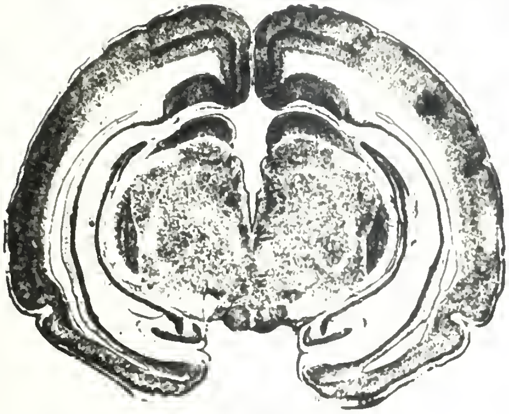
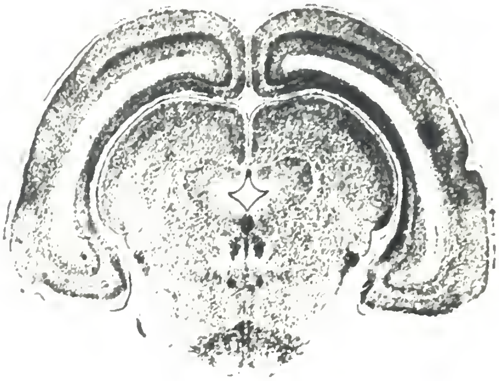
[1] Figure 16 shows a series of sections through a normal brain at approximately the same levels as those chosen to illustrate the lesion. This may be used by the reader as a standard against which to compare the lesion cases.

Figure 16. Selected Cresyl Violet Stained Sections Through the Superior Colliculus of a Normal Tree Shrew. Sections 88 and 118 are at the rostral and caudal borders, respectively, of the superior colliculus.

TUPAIA 98



88



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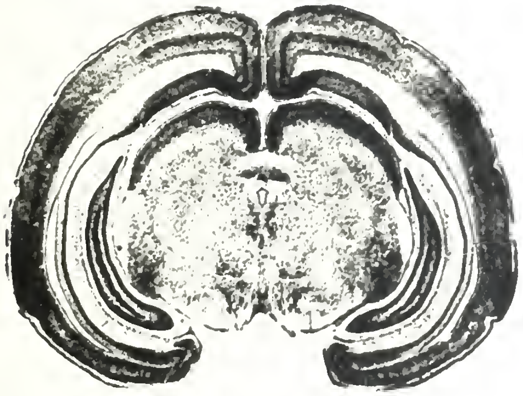

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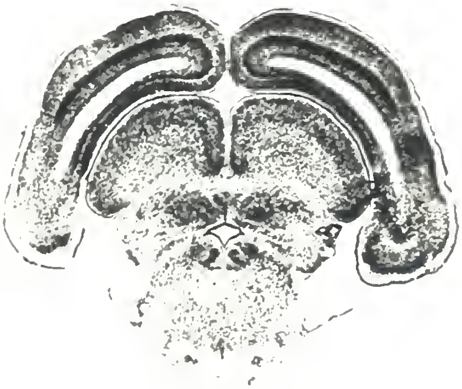
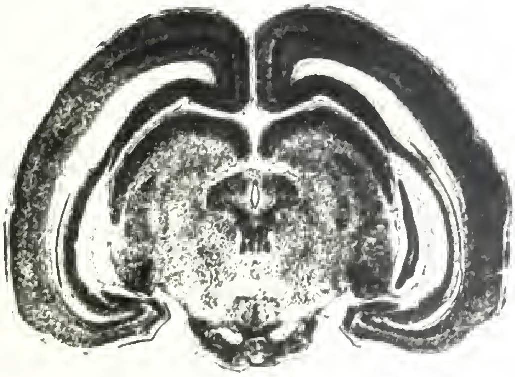


114



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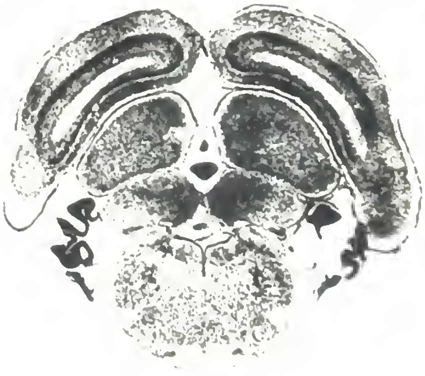
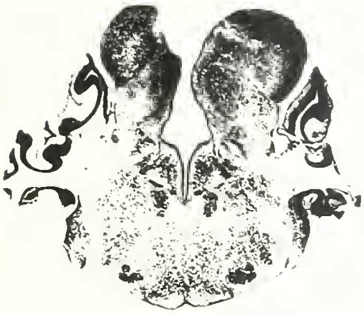


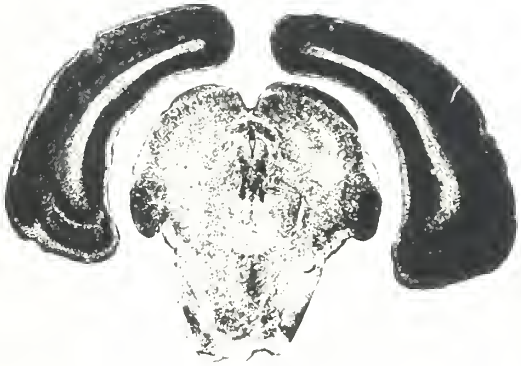
118

Figure 17. Selected Cresyl Violet Stained Sections Illustrating the Superficial Bilateral Ablation of the Superior Colliculus in Tupaia 300. Tupaia 299 had a similar, although slightly more extensive, lesion. In both cases, damage was almost exclusively restricted to the first three layers of the superior colliculus.

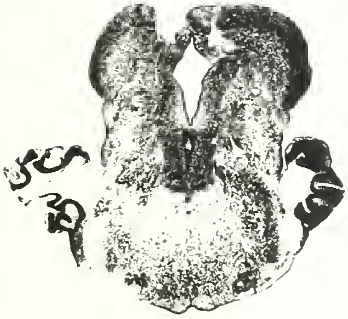
TUPAIA 300



20



38



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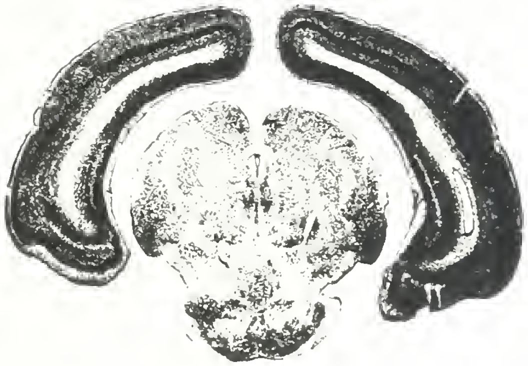
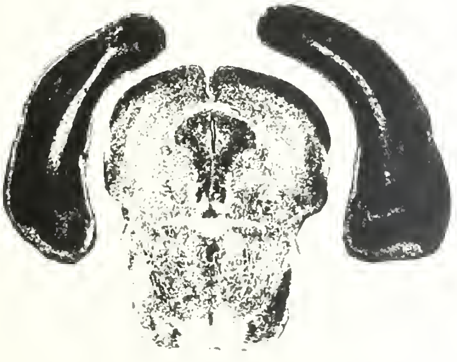
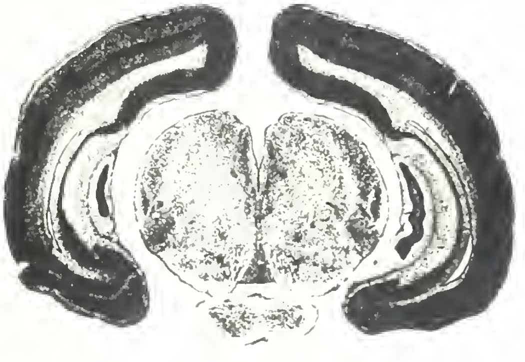


40



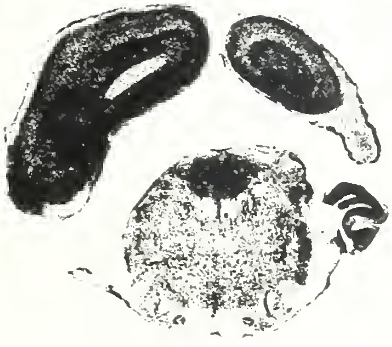
34



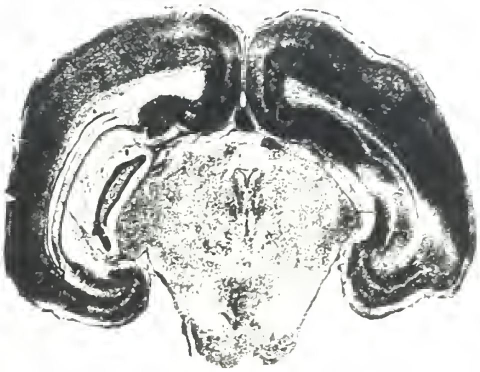
46

Figure 18. Selected Cresyl Violet Stained Sections Illustrating the Deep and Complete Bilateral Ablation of the Superior Colliculus in Tupaia 328. This lesion included damage to the inferior colliculus, pretectum, central grey, and tegmentum. There was also damage to the caudal thalamus, particularly to the dorsal lateral geniculate and pulvinar on the right and to the left half of the cerebellum (not shown). Tupaia 327, 329, 393, and 395 had (with some exceptions) similar lesions to those shown for Tupaia 328. See text for details.

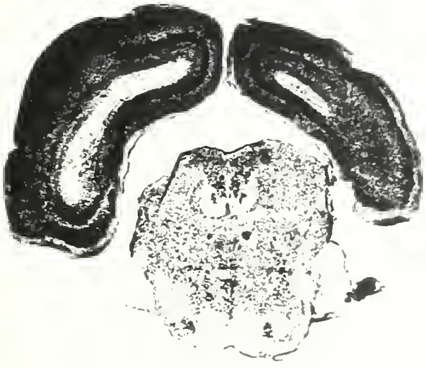
TUPAIA 328



37



49



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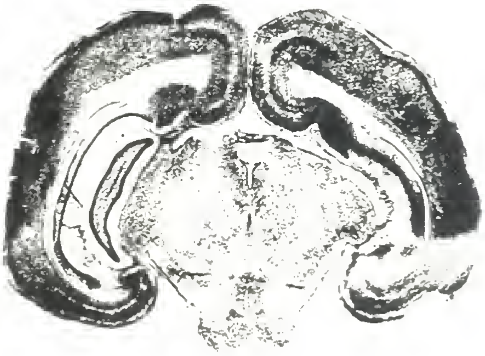

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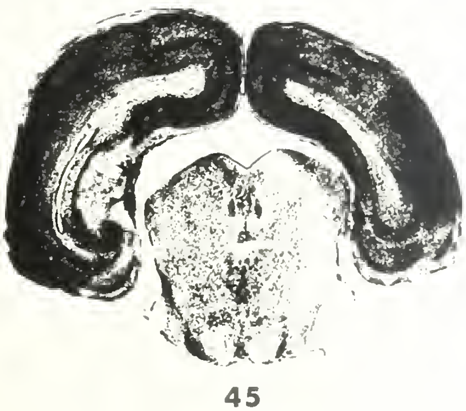

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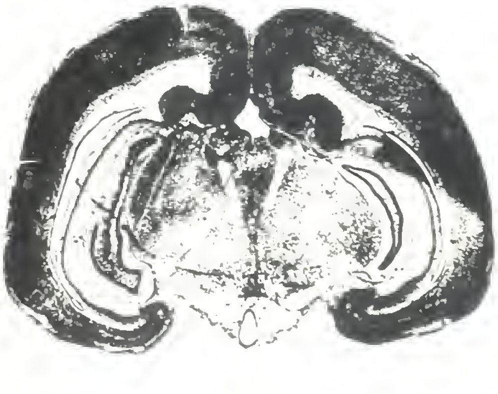

55

extensive than those just described (see Figure 19). In particular, there was less damage to the pretectum, central grey, and caudal thalamus, and no damage to the cerebellum. In Tupaia 215 a small portion of both colliculi may have been spared.[1] In Tupaia 211 the lesion was slightly more extensive than in 215 and included all of the superior colliculus and more of the pretectum. In both Tupaia 211 and 215, there was slight damage also to the medial wall of the cortex.

Of the eight animals only one, Tupaia 223, had a lesion of intermediate size (see Figure 20). It should be recalled that this animal was the only animal in the group (other than the two which looked normal) which retained some ability to follow a moving target. In this animal, the anterior and lateral portions of the superior colliculi were left intact, particularly on the right, while the more posterior and medial parts were almost totally removed. The lesion in this animal also included a small amount of damage to the pretectum, inferior colliculus, and anterior cerebellum (not shown) and a moderate amount of damage to the central grey.

Comparison between neonatal and adult lesions of the superior colliculus. There were no obvious behavioral differences between the effects of comparable lesions of the superior colliculus in neonatal versus adult

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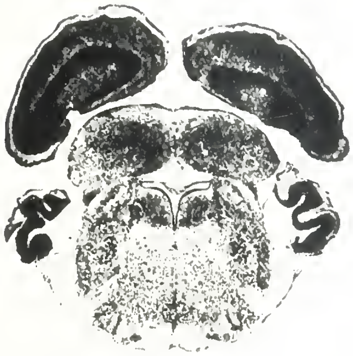
[1] Following extensive midbrain lesions, it is often difficult to define the exact boundaries between areas. In the case of Tupaia 215, it was difficult to tell the exact boundary between the deep layers of the superior colliculus and the pretectum.

Figure 19. Selected Cresyl Violet Stained Sections Illustrating the Extensive Bilateral Ablation of the Superior Colliculus in Tupaia 215. This lesion completely removed all of the superior colliculus with the possible exception of a portion of the deep layers anteriorly. There was also some invasion of the posterior thalamus, particularly on the right side, and the pretectum, central grey, and posterior medial wall of the cortex on both sides. This animal had a very similar lesion to that of Tupaia 211 (not illustrated) with the latter being slightly more extensive. Both animals underwent surgery as adults.

TUPAIA 215



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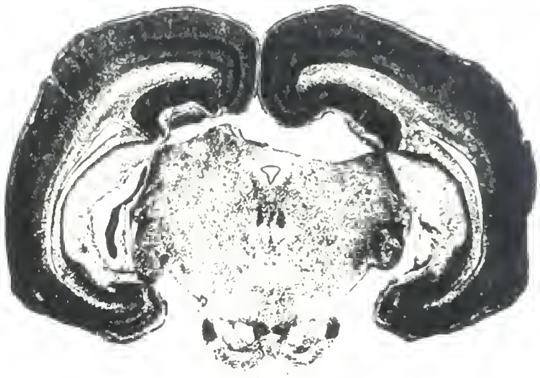

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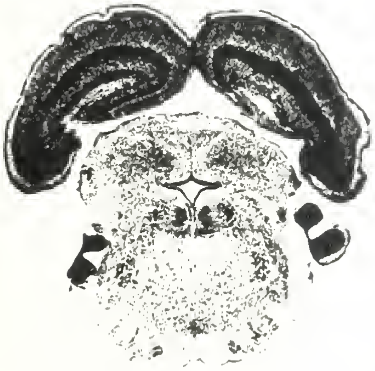

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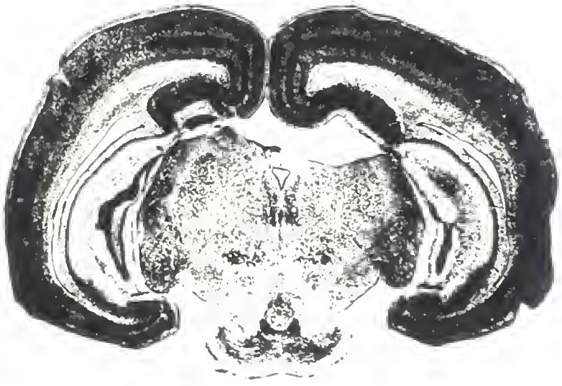

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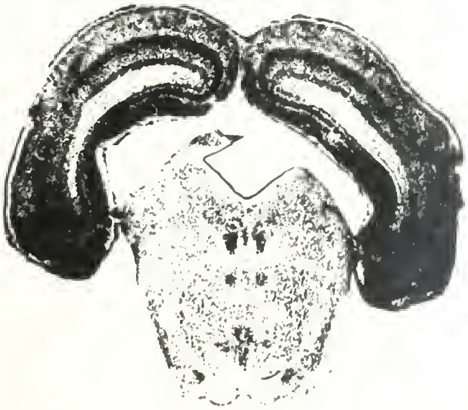

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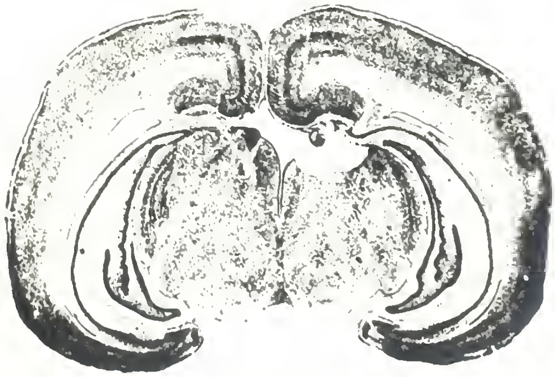

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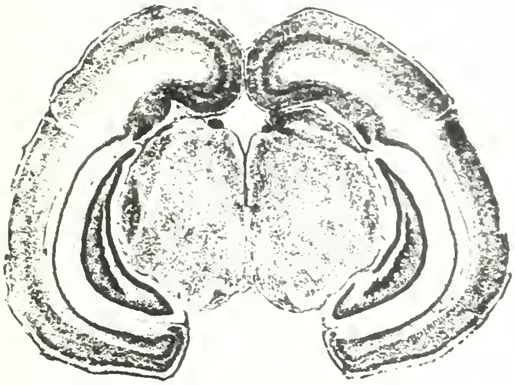
Figure 20. Selected Cresyl Violet Stained Sections Through the Large but Incomplete Superior Colliculus Lesion in Tupaia 223. This animal had the smallest lesion of the three animals which underwent surgery as adults. Note that anterior and lateral portions of the superior colliculus remained intact, particularly on the right. There was slight damage to the pretectum, central grey, and inferior colliculus.

TUPAIA 223



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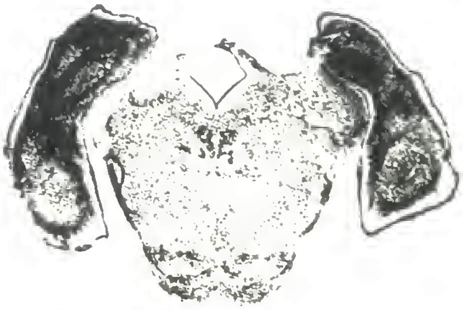

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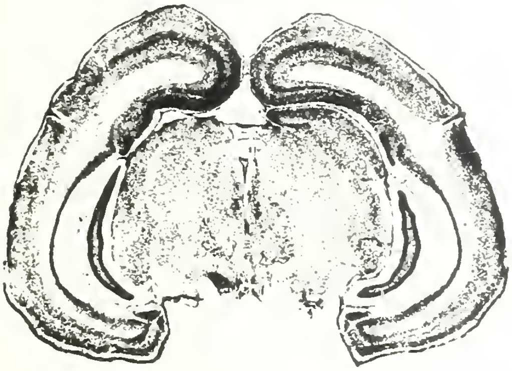

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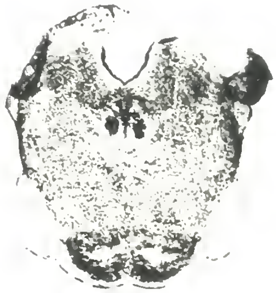

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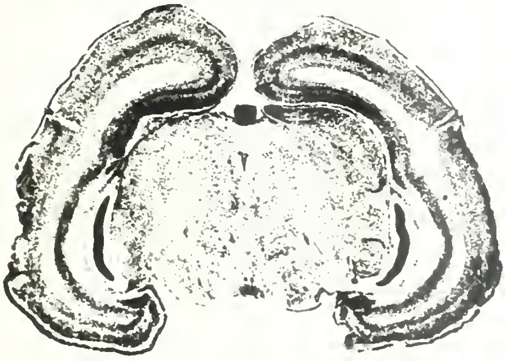

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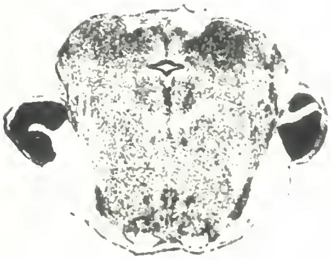

103

animals. Nevertheless, superior colliculus lesions made in neonates appeared to cause transneuronal degenerative changes and a shrinkage of the pulvinar,[1] which was not evident after the lesions were made in adults. Early lesions of the superior colliculus also appeared to cause the development of an anomalous retinal projection to the pulvinar not seen in normal animals or in animals which underwent surgery as adults (Casagrande, Hall, & Diamond, 1972). Schneider (1970) observed a similar anomalous projection in the hamster following neonatal superior colliculus lesions. Schneider also found that, following a superficial lesion of the superior colliculus in the infant hamster, retinal fibers terminated in the deeper layers where they would ordinarily not be found. Moreover, he found that when such lesions were made unilaterally some retinal fibers now decussated and terminated in the remaining superior colliculus. Neither of these anomalous projections were observed in the tree shrews involved in the present study. Comparison of the retinal projections to other areas following either neonatal or adult lesions of the superior colliculus in the tree shrews did not reveal any obvious differences although, in some of the neonatal cases, there appeared to be a slight increase in the terminal projections to a part of the pretectum.

In addition to the above, the retinas of several animals with and

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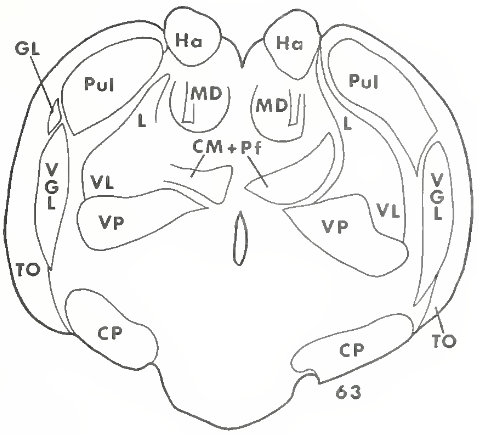
[1] The pulvinar nucleus of the tree shrew receives its major projection from the superior colliculus (Abplanalp, 1970; Casagrande et al., 1972; Harting, Hall, & Diamond, 1973).

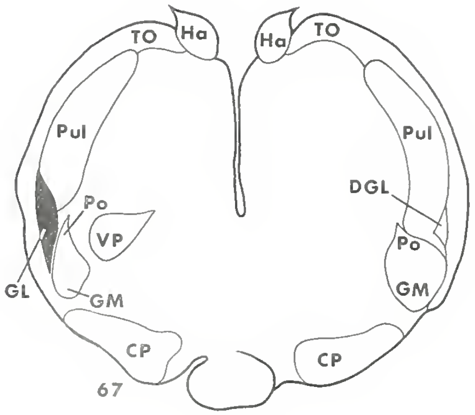
without lesions of the superior colliculus were compared. Since heavy damage to the superior colliculus, of necessity, would cause direct damage to the axons of ganglion cells, one might find some change in these cells or a cell loss. However, no obvious differences were observed between the retinas of four of the animals (one normal, one with a lesion as an adult, two with lesions as neonates) which were examined.

Lesions of the visual cortex. The distortions which occurred following neonatal lesions of the striate cortex in Tupaia 303, 304, and 323 made it extremely difficult to reconstruct these lesions accurately. The best estimate that could be made of the extent of damage was determined by a careful examination of retrograde degenerative changes within the thalamus. The criteria for determining such changes has been described previously in detail (see Diamond et al., 1970). Evidence of spared remnants of the dorsal lateral geniculate was found in two (303, 304) out of the three animals (see Figure 21), indicating that parts of the striate cortex had remained intact. In all three cases, the thalamus appeared distorted due to the apparent disappearance of much of the degenerated portions of the dorsal lateral geniculate. Such changes following neonatal damage to the visual cortex have been described previously in the hamster (Schneider, 1970). These changes lead to a peculiar situation where, due to the loss of the dorsal lateral geniculate nucleus, the ventral lateral geniculate nucleus now comes to lie next to the pulvinar. Such changes are not observed in tree shrews when the lesions of the visual cortex are

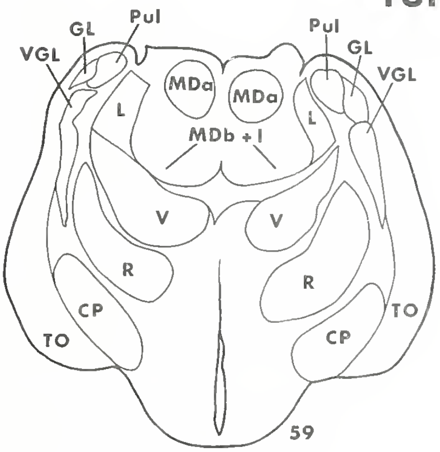
Figure 21. Drawings of Selected Thalamic Sections from Tupaia 303, 304, and 323. These animals received bilateral lesions of striate cortex 3 days after birth. Note that most of the dorsal lateral geniculate has disappeared. Of the remaining pieces, those which showed severe retrograde changes are depicted in black. The following abbreviations are used: CM = centromedian nucleus; CP = cerebral peduncle; GL = dorsal lateral geniculate body; GM = medial geniculate body; GP = griseum pontis; Ha = habenula; I = intralaminar nuclei; IP = interpeduncular nucleus; L = lateral nucleus; MD = mediodorsal nucleus; MDa = mediodorsal nucleus Division A; MDb = mediodorsal nucleus Division B; N. III = oculomotor nucleus; Pf = parafasicular nucleus; Po = posterior nucleus; Pul = pulvinar nucleus; R = reticular nucleus; RN = red nucleus; V = ventral nucleus; VGL = ventral lateral geniculate body; VL = ventrolateral nucleus; VP = ventroposterior nucleus.

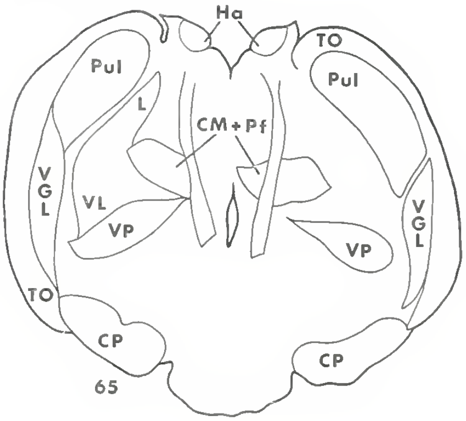
TUPAIA 303



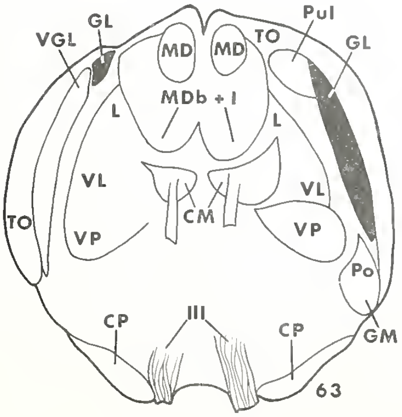


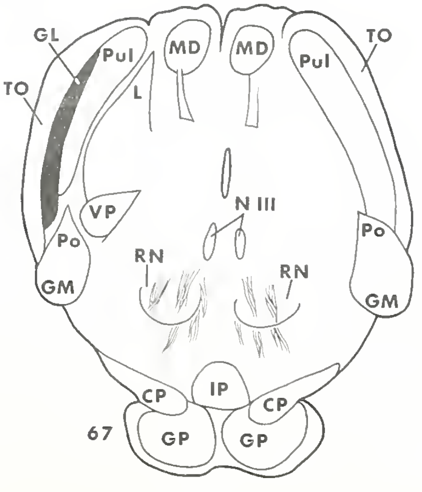
TUPAIA 304





TUPAIA 323





made when the animals are adult.

Conclusions

The results of this experiment have shown that the superior colliculus of the tree shrew plays a role both in visual guidance and visual discrimination. Furthermore, these results suggest that visual guidance deficits following damage to the superior colliculus are dependent upon the depth of the lesion. Total or nearly total removal of the superior colliculus, regardless of the animals' age at the time of surgery, produced a condition which made the animals appear "blind." These animals were grossly impaired in their ability to orient to and follow visual stimuli. In contrast, animals with superficial lesions appeared completely normal on these tests.

However, both superficial and deep lesions produced similar deficits in visual discrimination. All of the animals, regardless of the depth of the lesion, failed to discriminate the orientation of triangles and exhibited difficulty in the discrimination of color, particularly when paired with an achromatic stimulus. Yet, three animals with striate cortex lesions (surgery performed in infancy) easily performed these color tasks replicating the results of a previous study (see Snyder et al., 1969).

Finally, the three animals who easily learned preoperatively to distinguish disks of different sizes were unable to do so following damage to the superior colliculus (all three had large deep lesions). The deficits

following lesions of the superior colliculus could not be attributed to some general dementia since all eight of the animals were easily able to learn to discriminate light from dark and horizontal from vertical stripes.

EXPERIMENT II: NEUROLOGICAL TESTS AND TESTS OF VISUAL GUIDANCE

It was clear that the results of the observations of visual guidance, as well as the formal discrimination training in Experiment I, posed a number of problems. The behavioral observations of the animals had revealed what appeared to be a correlation between the degree of blindness and lesion size: two of the animals appeared normal and the rest did not. What was needed now was a more rigorous test which would in some way quantify these deficits. Furthermore, it was apparent from observing the animals with the largest lesions that, although they did not react to threatening gestures, they did appear to be able to avoid obstacles, a situation which again suggested that a more controlled test was necessary to determine precisely the nature of the deficit. Therefore, two more tests and more animals were added as a part of a second experiment.

Method

Subjects

The main group of eight animals described in Experiment I were also subjects of the present experiment. The animals which were added

included eight animals with lesions of the superior colliculus (five bilateral and three unilateral lesions), three animals with lesions of striate cortex as neonates (these animals were also subjects in Experiment I), and five normal animals. All of the additional animals were born in the laboratory, hand reared from birth, and cared for as described in Experiment I.

Neurological tests

Pupillary reflexes and eye movement. These tests were all conducted in a dark room with the animal held firmly in the hand of the experimenter. The size and speed of constriction of each pupil was tested with the light of an opthalmoscope. Each eye was tested separately and any asymmetry of response recorded. At the end of the tests the room lights were turned on and the animals were allowed to light adapt for a few minutes, after which the size of each pupil was again observed. During these tests records were also kept of any spontaneous eye movements.

Visual following and orientation. These tests were conducted in each animal's home cage, which was located in a large, well-lighted room.[1] Prior to the beginning of the tests, each subject was pretrained to come to the front of his cage and remain at the edge of the open entrance for a wax worm reward. The experimenter either stood or

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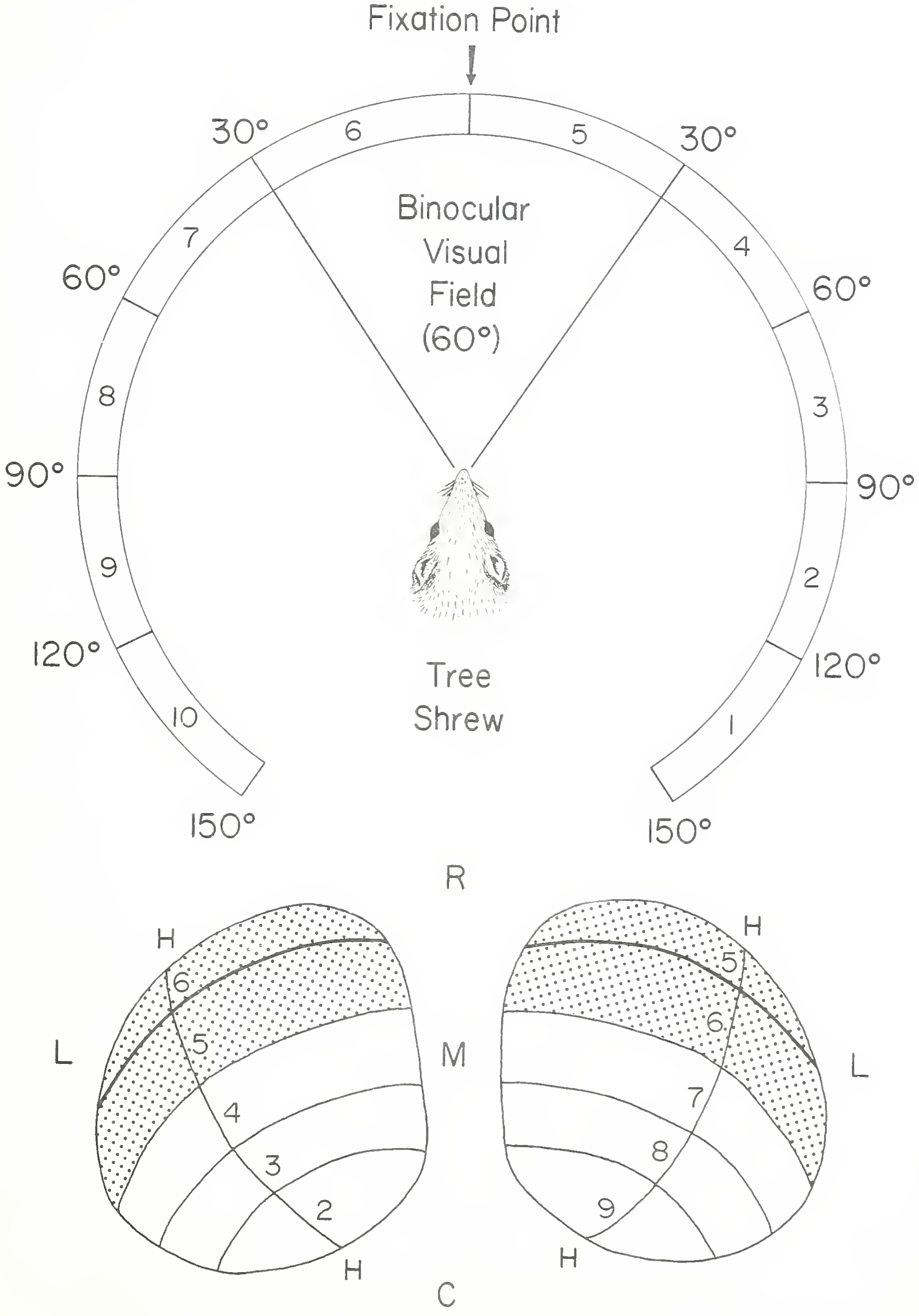
[1] During these tests all animals were maintained at 85 to 90% of their ad libitum feeding weights on a diet of cat chow and water.

remained seated in front of the cage and offered the reward at the end of a pair of forceps. Testing was begun only after the subject readily approached the front of his cage and remained there calmly for a number of rewards. The first test measured visual following by requiring the animal to track the worm reward as it moved away from the center of the field along a vertical line up or down, or to follow it as it moved in a horizontal line either from left to right or from right to left. To test visual orientation a reward was first held directly in front of the animal to attract and hold its attention at a central point marked "fixation point" in Figure 22. Then a second reward was brought into a part of the visual field and the first reward moved out of reach. In this situation a normal animal will immediately orient to the closer of the two rewards. The animal was rewarded intermittently at either position. The second reward could appear randomly in one of nine possible positions in the visual field of either eye as follows: First, within 30 degrees of the center of gaze either at (a) eye level, or (b) 20 degrees above (upper fields) or (c) 20 degrees below (lower fields) eye level. Second, between 60 and 90 degrees at the same three positions for each eye. And third, beyond 90 degrees again at the same three positions for each eye. During each session the worm was presented in each position five times. Each animal was tested for a total of five consecutive daily sessions. Thus, at the end of five days of testing the subject had received a total of 25 presentations of the stimulus in all parts of the visual field and an additional

Figure 22. Schema to Show the Visual Field of the Tree Shrew and Its Representation on the Superior Colliculi from a Dorsal View. The map of the visual field on the superior colliculi is taken from Lane, Allman, and Kaas (1971). Numbers 1 and 10, which appear in the extreme periphery of the field are represented on the caudal pole, not visible from the surface. The stippled zone represents the area of binocular overlap which has an expanded representation on the superior colliculus. This was the area which was most often spared during an ablation. Note that the entire field of each eye is represented on the contralateral colliculus. The vertical median is depicted as a heavy line between 5 and 6 at the anterior border. The following abbreviations are used: C = caudal; H = horizontal meridian; L = lateral; M = medial; R = rostral.


Fixation Point
30°
6
5
30°
Binocular
Visual
Field
(60°)
7
4
60°
60°
8
3
90°
90°
9
2
120°
120°
10
1
Tree
Shrew
150°
150°
R
H
6
5
4
3
2
H
L
M
H
5
6
7
8
9
H
L
C

25 presentations of the stimulus moving either up, down, or to the right or left. At the end of this testing period each animal was given an additional day with the same sequence of tests while wearing opaque contact occluders.[1] This allowed some estimate to be made of the animal's ability to orient using nonvisual cues such as olfaction.

Localization of auditory and somatosensory stimuli. Some of the animals used in the previous tests were also given tests of their ability to localize auditory and somatosensory stimuli. Initially, an effort was made to give all of the animals this test; however, only some of the animals would tolerate wearing opaque contact occluders for a sufficient length of time to complete the tests. The use of occluders proved to be essential for such tests since normal tree shrews prefer, if possible, to use visual cues for localizing stimuli. The group which was tested included eight animals with bilateral lesions of the superior colliculus (215, 223, 309, 310, 327, 328, 394, 395), three animals with unilateral lesions of the superior colliculus (387, 388, 389), three animals with lesions of striate cortex (303, 304, 323), and two normal animals (261, 403).

For these tests the animals were placed in a large box open at the top. Each animal was allowed a few minutes of adaptation to the box

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[1] The occluders were fashioned from ten mill thick sheets of black acrylic. They were designed to fit over the entire eye. The eye itself was protected with Neosporan opthalmic ointment.

and the opaque occluders before testing began. After this period of adaptation the animals were tested first on the auditory localization test.[1] This test consisted of 15 click stimulus presentations. For each animal the click stimuli were presented randomly five times each in three positions (to the right, left, or overhead) and the animals' responses were recorded. Later each animal was tested for localization of somatosensory stimuli (light touch, prick, or pinch) applied separately to each paw, the sides of the face, the shoulders, and the hips.[2] As in the auditory test, the stimuli were presented randomly five times at each location (in this case, on the body surface) and all responses recorded. No rewards were administered for responses to auditory or somatosensory stimuli.

Barrier tests

Nine animals with lesions of the superior colliculus which had exhibited deficits in their ability to orient to or to visually follow moving targets were tested for their ability to move through openings in a serially arranged set of three barriers. Their performance was compared with the performance of three normal animals and also with three animals with striate lesions. The apparatus, shown in Figure 23a,

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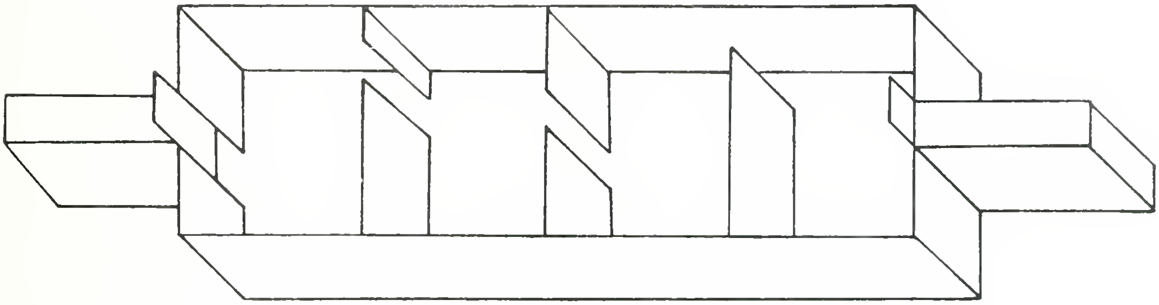
[1] A toy Halloween clicker served as the stimulus.

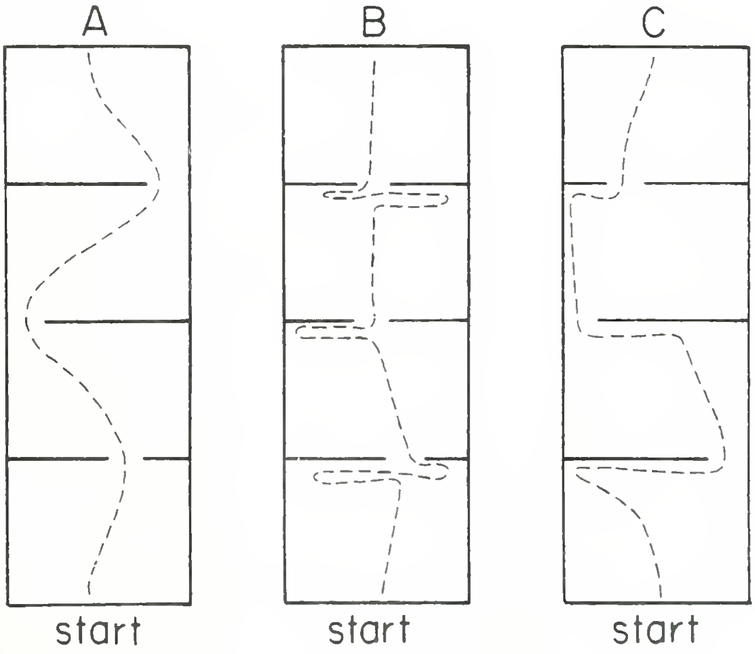
[2] The animal was touched lightly with the end of a hemostat. Painful pinching stimuli were produced with a hemostat and pricks with the end of a 27-gauge needle.

Figure 23a. Drawing of the Barrier Apparatus as Viewed from the Top. The apparatus was divided into four compartments by interchangeable panels. Start and goal boxes were located at either end. The animals were required to run through the openings in the barriers to the other end of the apparatus for food reinforcement. The position of the openings in the barriers were varied randomly from trial to trial.

Figure 23b. Types of Errors Scored in the Barrier Tests. The dashed lines represent paths of animals as they ran through the apparatus starting at the bottom. (A) This shows a representative path which was scored as errorless. (B) This shows a path of an animal which scored three "proximal" errors. (C) This shows a path of an animal which scored three "distal" errors. See text for details.

Test for Perception of Barriers





consisted of a 48-in. x 16-in. x 6-in. black Plexiglas box. Interchangeable goal and start boxes with doors were connected to the apparatus at either end. The apparatus was covered with a set of four clear sheets of Plexiglas and was divided into four compartments by three sets of interchangeable white Plexiglas barriers. Light was provided by two 150-watt bulbs located above the apparatus. For the first test these barrier panels of different sizes were arranged so as to produce a 2 1/2-in. slot in any one of five equally spaced positions starting at the extreme edges. In a second test these barriers were replaced with another set which contained holes 2 1/2 in. in diameter. The holes were also designed so that they could appear in one of the same five positions and, in addition, could be either in a position 1 in. or 3 in. above the floor of the test chamber.

The main purpose of the tests with the barriers was to provide some formal measure of the animal's ability to orient to and move itself around obstacles while its environment remained stable. No learning was required. The subject was simply allowed to travel at its own pace through the openings from one end of the apparatus to the other to receive a food reward (two wax worms) in the goal box. During the tests all animals were maintained at 85 to 90% of their ad libitum feeding weights on a diet of cat chow and water. The subjects were transported to the apparatus from their home cages in one of the "start-goal" boxes which could be detached from the apparatus. The animals were not given any pretraining in the apparatus; thus, all animals were completely naive in

the situation from the beginning of the test. In Test 1 the animals were required to navigate through slots in the barriers. The animals were tested for 20 days, with five trials daily for the first 5 days and ten trials daily for the next 15 days. On each trial in this task the subject was given a different combination of slot positions (100 different combinations were used). On each trial the animal was released from the start box at the end of the apparatus. The time it took him to cross the apparatus was measured by a clock timer attached to two photocells at either end of the apparatus. As the animal moved through the barriers his path was recorded as accurately as possible.[1] In this test an animal could commit an "error"[2] in visual guidance in one of two ways. If the animal did not move directly to the opening, it scored a "distal" error. If the animal did approach the opening but then did not proceed through it but rather paced back and forth along the barrier, it was called a "proximal" error. Typical paths that an animal would traverse while making each of these errors is shown in Figure 23b. At the termination of each trial, the goal box became the start box for the succeeding trial, and so forth. At the end of 20 days of testing in this situation, the subjects were given 5 days

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[1] Hand-drawn records were made of the animal's path.

[2] An arbitrary limit of two errors (one "proximal" and one "distal") was set for each compartment since it was impossible to judge multiple errors accurately enough from the hand-drawn records. Therefore, an animal could commit a maximum of six errors, two for each compartment, in any one trial.

(ten trials a day) in the same situation, only this time while they wore opaque contact occluders. This allowed some estimate to be made of the subject's ability to navigate through the barriers using nonvisual cues.

Essentially the same thing was required of the animals in Test 2 as just described for Test 1, the difference being that the slots were now replaced by 2 1/2-in. diameter holes. The animals were tested in this situation for 12 days, five trials a day for the first 2 days and ten trials a day for the remainder of the period. Where appropriate, the performance of the animals on these tests was compared by means of the Kruskal-Wallis one-way analysis of variance (Siegel, 1956).

Surgical and histological procedures

Eleven of the subjects used in the present experiment (eight with lesions of the superior colliculus and three with lesions of striate cortex) were also subjects in Experiment I. Therefore, the surgical and histological procedures for these animals have already been considered in detail in the Method section of Experiment I. Essentially the same surgical and histological procedures were employed with the remaining subjects in Experiment II. Of these remaining animals five were selected for analysis of possible changes in the distribution of retinal fibers which might have resulted from their lesions. These animals underwent removal of one eye (310, 387, 393, 395) or both eyes (388) 3 to 5 days prior to sacrifice. Their brains were processed according to the

procedures already described in Experiment I.

Results

Neurological tests

Pupillary reflexes and eye movements. Changes in pupillary response were noted only in those animals with significant damage to pretectal regions. These changes constituted a slight to moderate dilatation of the pupil (the more extensive the lesion, the wider the pupil) and a sluggishness of response (see Table 2). All animals, regardless of lesion size, appeared to be able to move their eyes, although it was not possible to determine whether these spontaneous movements were well directed.

Visual following and orientation. Formal tests of visual following and orientation yielded results which supported the conclusions of the behavioral observations reported in Experiment I. The animals which had superficial lesions of the superior colliculus were behaviorally indistinguishable from the normal tree shrews, while the animals with deep lesions had severe deficits.

Table 3 summarizes the scores of all of the animals on the tests of visual following. Each animal was given a total of 25 presentations of the stimulus moving in each of the four directions (left, right, up, and down). Similarly, each animal was given 25 presentations of a stationary stimulus held at each of 18 possible positions in the field. The results of

Table 2

Pupillary Response and Size

Animal	Lesion	Left Eye	Right Eye
261	None	NS, N	NS, N
304	Striate lesion as neonate	NS, N	NS, N
303		NS, N	NS, N
323		NS, N	NS, N
299	Superficial tectal lesion as neonate	NS, N	NS, N
300		NS, N	NS, N
309	Deep tectal lesion as neonate (lesion incomplete)	NS, N	NS, N
310		NS, N	NS, N
394		d, S	NS, N
395	Deep tectal lesion as neonate (lesion complete or nearly complete)	NS, N	NS, S
393		d, S	d, S
329		D, S	D, S
327		d, S	D, S
328		D, S	D, S
211	Deep tectal lesion as adult	d, S	d, S
215		d, S	d, S
223		NS, N	NS, N
387	Unilateral right tectal lesion as neonate (deep lesions)	NS, N	NS, N
388		NS, S	NS, N
389		NS, S	NS, N

Note.--NS = normal size; d = slightly dilated; D = widely dilated; N = normal response; S = sluggish response.

Table 3

Performance Scores in Test of Visual Following

		Number of Correct Responses in 25 Presentations			
Animal	Lesion	Up	Down	R-L	L-R
261	None	25	25	25	25
225		25	25	25	25
222		25	25	25	25
304	Striate lesion as neonate	25	25	25	25
303		25	25	25	25
323		25	25	25	25
299	Superficial tectal lesion as neonate	25	25	25	25
300		25	25	25	25
309	Deep tectal lesion as neonate (lesion incomplete)	22	25	16	11
310		7	23	5	7
394		11	6	12	8
395	Deep tectal lesion as neonate (lesion complete or nearly complete)	0	16	0	0
393		0	5	0	0
329		0	2	0	0
327		0	3	0	0
328		0	6	1	0
211[a]	Deep tectal lesion as adult	-	-	-	-
215		0	5	0	2
223		0	25	5	6
387[b]	Unilateral right tectal lesion as neonate (deep lesions)	25	25	18	0
388		25	25	0	0
389		20	20	0	0

Note.--The direction of stimulus movement is indicated at the top of each column. Right (R), Left (L) are with reference to the animal.

[a] 211--animal extremely wild, refused to submit to full test. However, she showed no sign of ability to follow stimulus on the few trials on which the animal did cooperate.

[b] The three animals with unilateral lesions all oriented to the stimulus on the right in the R-L condition but did not follow it (with the exception of 387). In the L-R condition they began to follow the stimulus only if it approached the midline and crossed over on the right.

this test are summarized in Table 4.

With two exceptions, those animals with the largest and deepest lesions showed little or no response either to moving stimuli or to stationary stimuli in any part of the visual field. Only on occasion was a correct response seen and then only when the stimulus was in a region closest to the animal's nose. One possible interpretation of these few responses is that they were not visually guided at all. In support of this interpretation was the finding that some of these animals could on occasion (one presentation in five) orient to the stimulus while wearing opaque contact occluders.

The two exceptional cases (215, 395) were able to orient better than what might be predicted based on a sparing of part of the superior colliculus or on nonvisual cues.[1] Tupaia 215 was able to orient to, but could not follow, stimuli within 30° of the midline. When tested in this part of the field Tupaia 215 performed at least as well as Tupaia 223, whose lesion spared approximately one-quarter of the rostral superior colliculus. Even more puzzling was the ability shown by Tupaia 395. This animal was clearly able to orient to a worm held within 30° of the midline on its left and to follow it into the lower part of the field. Possibly other areas such as the pretectum or central grey were responsible for the recovery

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[1] A small piece of the deeper layers of the anterior superior colliculus remained intact in Tupaia 395. In Tupaia 215 a portion of the deeper layers may have also remained in the anterior part of the superior colliculus (see histological results).

Table 4

Performance Scores in Test of Visual Orientation

		Number of Correct Responses in 25 Presentations																	
		Left Eye									Right Eye								
		Within 30°			Between 60°-90°			Beyond 90°			Within 30°			Between 60°-90°			Beyond 90°		
Animal	Lesion	H	U	L	H	U	L	H	U	L	H	U	L	H	U	L	H	U	L
261	None	23	25	25	24	24	25	24	25	25	25	25	25	24	24	23	23	24	25
225		25	25	25	25	25	25	22	23	25	25	25	25	22	25	24	25	24	25
222		25	25	25	24	25	25	25	25	22	25	24	25	25	25	25	22	23	25
304	Striate lesion as neonate	25	25	24	25	25	25	25	25	25	25	25	25	25	24	25	25	24	25
303		25	25	25	24	25	24	25	25	24	25	25	24	25	25	25	25	24	24
323		25	25	25	24	24	24	25	24	25	22	24	24	23	24	22	24	23	24
299	Superficial tectal lesion as neonate	23	23	25	25	24	25	22	20	22	25	25	25	24	25	25	22	23	19
300		25	25	24	25	25	25	24	22	23	25	24	25	25	23	25	25	24	23
309	Deep tectal lesion as neonate (lesion incomplete)	24	24	24	15	14	16	0	2	0	18	17	20	12	12	10	1	2	3
310		21	23	23	8	11	11	3	0	3	19	22	24	8	6	9	0	0	5
394		23	21	22	21	14	15	10	10	7	21	19	20	14	9	12	3	2	6

395	Deep tectal lesion as neonate (lesion complete or nearly complete)	19	5	18	9	0	16	0	0	11	1	0	9	0	0	3	0	0	0
393		10	7	8	9	1	6	0	0	0	5	3	6	4	0	2	0	0	0
329[a]		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
327		2	0	9	0	0	3	0	0	4	0	0	1	0	0	2	0	0	1
328		6	0	5	0	1	3	0	0	1	8	0	4	1	0	3	0	0	2
211[b]	Deep tectal lesion as adult	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
215		20	13	24	2	3	8	0	1	0	19	14	13	0	0	9	0	0	0
223		17	14	16	5	2	2	0	0	0	20	17	15	4	4	6	0	0	0
387	Unilateral right tectal lesion as neonate (deep lesions)	22	24	22	7	16	7	1	0	4	25	25	25	25	25	25	23	22	25
388		19	21	19	2	8	11	0	1	1	25	25	25	25	25	25	24	25	25
389		21	20	19	8	10	0	0	1	0	25	25	23	25	25	24	23	24	25

Note.--H = at eye level; U = upper visual field; L = lower visual field.

[a] 329 died before testing was completed, but appeared similar in behavior to 328.

[b] 211 was extremely wild, thus accurate testing proved impossible. In general, she seemed worse in visual orientation than either 215 or 223.

seen in these cases: the animals which showed little or no orienting ability in any part of the visual field always sustained heavy damage to both of these areas.

Animals with partial damage to the superior colliculus were able to orient to and follow visual stimuli in some but not all parts of their visual field. Generally the region where orienting responses were found lay within 30° of the midline (the region of binocular overlap). Electrophysiological study of the superior colliculus of the tree shrew has demonstrated that this part of the field has an expanded representation on the rostral part of the superior colliculus (Lane et al., 1971). This is just the region which was most often spared in the present experiments. Figure 22 shows a diagram of the representation of the visual field on the superior colliculus. Note the wide area of tissue devoted to the region of binocular overlap. Since the surgery was done either by looking directly down upon the superior colliculus or by a posterior approach, the regions which would be easiest to remove would be along the midline (representing the upper field) and at the caudal pole (representing the extreme periphery). It is therefore not surprising that when only a portion of the superior colliculus was ablated the portion of the visual field where orienting responses could not be elicited was most often in the upper field and in the extreme periphery.

The three animals with unilateral lesions of the right superior colliculus were all able to orient to and track stimuli in the visual fields

ipsilateral to the lesion but showed marked deficits in these abilities when stimuli were presented in the visual fields contralateral to the lesion, except for the region of binocular overlap. In the tests of visual following, the two animals (388, 389) with the largest lesions were both able to orient rapidly to a worm when it was presented ipsilateral to the lesion; but if it moved from this point toward the midline, they were unable to follow it. If, however, it was moving from the midline into the field ipsilateral to the lesion, they easily followed it into the far periphery. In fact, if the worm continued to move around these animals in the same direction (clockwise with respect to the animal), they would circle to keep up with it. The third animal (387), with a smaller lesion, showed some ability to orient to and follow stimuli presented in the visual fields contralateral to the lesion.

Finally, all three animals (303, 304, 323) with lesions of the striate cortex showed normal ability to orient to and follow visual stimuli.

Tests of auditory and somatosensory localization. The three animals with striate cortex ablations (303, 304, 323) were indistinguishable from the two normal animals (261, 403) on tests of auditory and somatosensory localization. In contrast, the animals with lesions of the superior colliculus showed either no deficit or severe deficits on both tests, depending upon the extent of the lesion. Tupaia 309, 310, 387, and 394 all responded as well as normals. All four of these animals had incomplete lesions of the superior colliculus with only a slight invasion of other

structures. The remaining animals exhibited difficulty in locating auditory and tactile stimuli. On the auditory test they showed an increased tendency to run or "freeze" instead of turning in the direction of the click. These same animals (particularly those with very extensive lesions) also consistently mislocated tactile stimuli (light touch or prick of the skin) particularly on the hips and hind feet, but also to a lesser degree on the forefeet and head, although touch of the vibrissae elicited normal head turning. If the skin was pinched hard on any area of the body, all animals except Tupaia 327 exhibited immediate and accurate localization of the stimulus. Only Tupaia 327 appeared unable to locate even a very painful pinch.

The most striking deficits in localizing auditory and somatosensory stimuli were seen in two animals with unilateral removal of the superior colliculus (388, 389). Auditory and tactile stimuli were consistently mislocated on the side contralateral to the lesion. The animals always tended to turn toward the side of the lesion regardless of which side the stimulus was presented. In spite of this, they were always able to accurately localize a prolonged pinch to the skin anywhere on the body contralateral to the lesion.

With respect to the tests of auditory and tactile localization, it should be mentioned that (without exception) all animals which exhibited deficits had at least some damage to the central grey and intercollicular

zones[1] lying adjacent to the superior colliculus. In five of these animals (327, 328, 388, 389, 395) there was also extensive damage to the inferior colliculus (see histological results). Damage to these areas may have contributed to the deficits. However, the damage to these areas was minimal in Tupaia 215 and 223, which had deficits, and Tupaia 394, which appeared normal, suggesting that damage to the superior colliculus was the major contributing factor.

In summary, the main results of the neurological tests showed: (a) that the animals with superficial lesions of the superior colliculus were able to locate accurately and follow all visual stimuli; (b) that in cases of incomplete but deeper lesions, the animals could orient to visual stimuli presented only in that part of the field represented on the spared portion of the colliculus; and (c) that animals with the most extensive lesions of the superior colliculus were unable to orient to and follow visual stimuli in any part of the field and showed mislocalization of auditory and somatosensory stimuli.

Barrier tests

From the first day, it was obvious that the animals were much less handicapped in the barrier tests than one might have predicted by watching them in the tests of visual following and orientation. Although they

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[1] The intercollicular nucleus and central grey of the tree shrew are known to receive afferent input from the dorsal column nuclei and spinal cord (Schroeder & Jane, 1971).

did make errors, one could not help but be impressed by the speed and ease with which they moved around and through the barriers. The only apparent difference in the way the animals moved was in the carriage of their heads. Normal animals tended to move their heads far more while running than did animals with lesions of the superior colliculus. Table 5 shows the total number of errors committed by each animal during the last 10 days of each of the tests. No statistically significant differences were found in the total number of errors committed in either Test I or Test II by the animals with superior colliculus lesions as a group when compared with the normal animals and with the animals with striate cortex damage. Also, there was no statistically significant difference between the groups in measures of latency in crossing the apparatus or in the types of errors committed.[1] In spite of this, it was clear from the scores that some of the animals with lesions of the superior colliculus did commit many more errors than any normal animal. When observing the animals' performance, it was obvious that some of these animals were handicapped by motor difficulties such as forced circling. In fact, Tupaia 327 often tended to get trapped in a compartment due to his fits of forced circling. Also, Tupaia 395 and 328 tended to occasionally bump into the barriers, something which was never seen in normal animals. All three of these animals had extremely deep lesions which also included

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[1] All of the animals (regardless of lesion) tended to make more errors when the openings were located at the extreme edges of the barriers or (in Test II) when the holes were located 3 in. above the floor.

Table 5

Total Number of Errors Scored During the Last 10 Days of Tests I and II With Barriers

Animal Number	Lesion	Number of Errors in Test I	Number of Errors in Test II
327	Tectal lesion as neonate	141	222
328	"	80	161
395	"	85	173
394	"	43	61
393	"	62	132
310	"	45	82
309	"	24	26
223	Tectal lesion as adult	64	148
215	"	23	41
304	Striate lesion as neonate	35	78
303	"	45	72
323	"	45	58
390	None	26	15
261	"	38	35
391	"	27	40

damage to the cerebellum (see histological results). Therefore, cerebellar damage may have explained in the latter cases why the animals made so many errors. However, there were animals which appeared to have no motor problems (Tupaia 393) yet did commit a large number of errors. Several comparisons were made in an effort to sort out which factors were contributing to the higher error scores in some of these animals. For one such comparison, all animals with complete or nearly complete lesions of the superior colliculus were compared as a group with all animals with incomplete lesions, and both of these groups were in turn compared with normal animals and animals with lesions of the striate cortex. Again there was no significant difference found between groups. There was also no significant difference between groups if those animals which were shown not to be able to orient to visual stimuli in neurological tests (327, 328, and 393) were compared as a group with the others, although all of these animals did make more errors than either normal animals or animals with striate lesions. Therefore, although some of the animals with lesions of the superior colliculus did make more errors than normals, other factors than simply the lesion of the superior colliculus appeared to be contributing to the effect. Since many other midbrain structures were also damaged in the latter cases, this again raises some question about the importance of areas other than the superior colliculus in visual guidance.

In addition to the above tests, some of the animals were run in

Test I for 5 additional days while wearing opaque contact occluders. This helped to give a picture of the animals' ability to navigate through the barriers without using visual cues. Table 6 shows a comparison of the performance on this test of these animals with and without visual cues. It is obvious from the scores that all animals, regardless of lesion, were significantly worse without sight than with it. Clearly, even the deepest lesion of the superior colliculus was not comparable to "blindness" in such a situation.

In summary, the most significant result of the barrier test was the finding that tree shrews with lesions of the superior colliculus could move themselves through openings in barriers and around obstacles even though they had previously been shown to be severely impaired on their ability to orient and to follow a visual stimulus. As a group, animals with complete or nearly complete lesions were not significantly different from normal animals and animals with striate lesions either on types of errors committed or latency to cross the apparatus in either Test I or Test II. However, for reasons which were not apparent, some of the animals with superior colliculus lesions made more errors than either normal animals or animals with striate lesions.

Histological results

Ten of the animals used in the present experiment were also subjects in Experiment I. For details of their histological examinations, see

Table 6

A Comparison of the Total Number of Errors Scored During the Last 5 Days of Test I With Barriers and 5 Additional Days on the Same Test in Which the Animals Wore Opaque Lenses

Animal Number	Lesion	Number of Errors Without Lenses	Number of Errors With Lenses
327	Tectal lesion as neonate	69	189
328	"	30	184
394	"	23	187
310	"	23	149
309	"	10	150
223	Tectal lesion as adult	29	168
304	Striate lesion as neonate	16	156
303	"	19	146
323	"	19	157
261	None	18	144

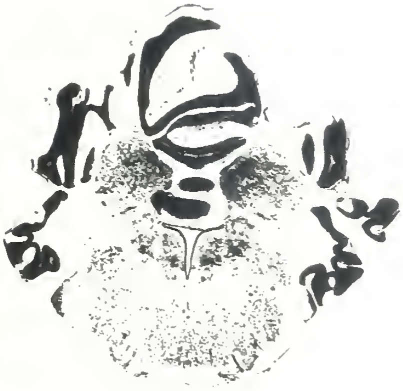
pages 12 and 13. Included in this group were two animals with superficial lesions (299, 300), one animal with an incomplete but deep lesion (223), five animals with complete or nearly complete lesions (211, 215, 327, 328, 329), and three animals with lesions of the striate cortex (303, 304, 323).

Of the remaining animals included in this experiment, two animals (393, 395) received very extensive bilateral lesions of the superior colliculus. The extent of their lesions was similar to that of Tupaia 328 shown in Figure 18 (p. 59) with three exceptions: First, a small portion of the deeper layers of the rostral superior colliculus on both sides appeared to be spared in Tupaia 395. Second, Tupaia 395 had extensive damage to the right rather than the left half of the cerebellum, as was the case in Tupaia 328. And, finally, Tupaia 393 had a less extensive lesion posteriorly which did not involve the cerebellum and involved only a small amount of the inferior colliculus.

Three animals were found to have large but incomplete lesions of the superior colliculus; and since the lesions were different in each case, separate illustrations have been included. Figure 24 shows the lesion in animal 309. In this animal approximately one-half of both superior colliculi remained undamaged. The lesion was restricted mainly to the medial and posterior parts of the superior colliculus and included a part of the central grey. Tupaia 394 (see Figure 25) had a more extensive lesion. In this animal, as in Tupaia 309, there was more damage to the postero-

Figure 24. Selected Cresyl Violet Stained Sections Through the Incomplete Lesion of the Superior Colliculus in Tupaia 309. Damage was restricted mainly to the caudal and medial aspects of the superior colliculus and dorsal portions of the central grey.

TUPAIA 309



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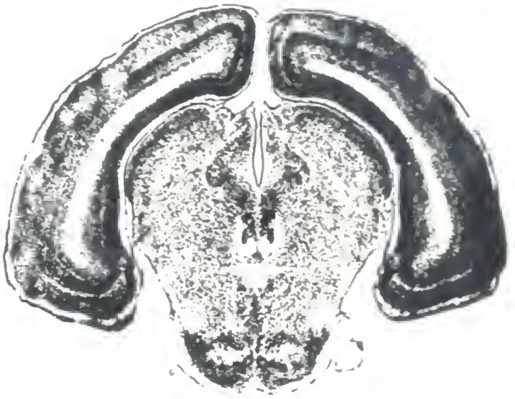

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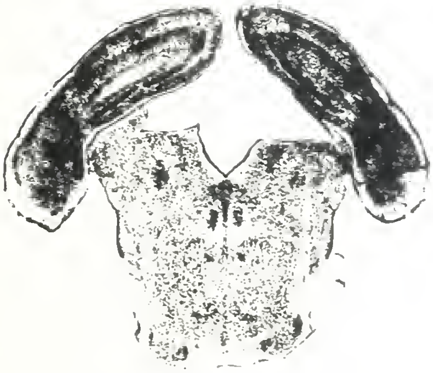

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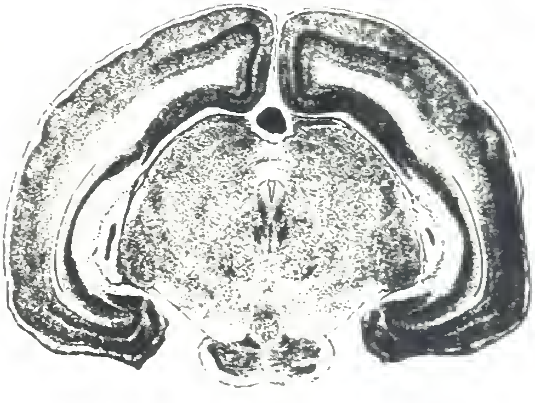

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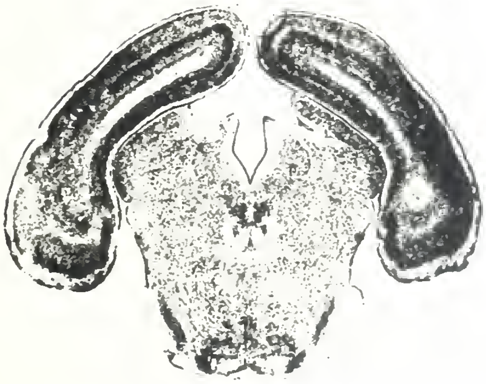

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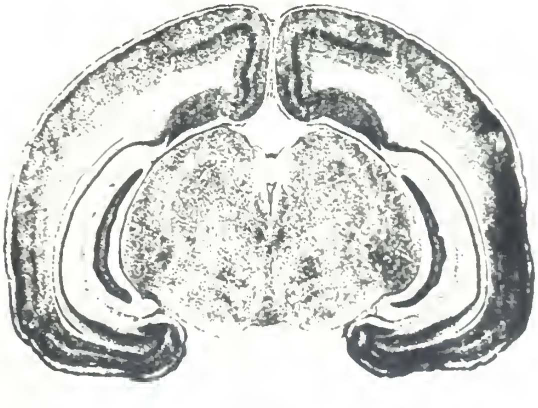

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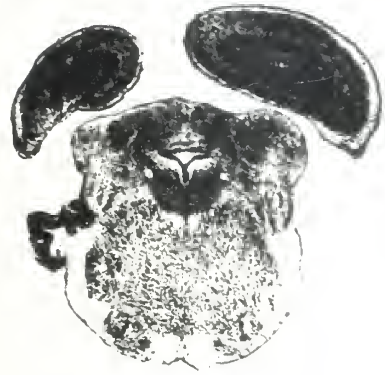
Figure 25. Selected Cresyl Violet Stained Sections Through the Incomplete Lesion of the Superior Colliculus in Tupaia 394. Most of the caudal and medial portions of both superior colliculi were removed. The left superior colliculus appeared to have a slightly more extensive lesion. The lesion also included damage to the superficial laminae anteriorly as well as slight damage to the pretectum, central grey, and inferior colliculi, particularly on the left and to the cerebellum on the right (not shown).

TUPAIA 394



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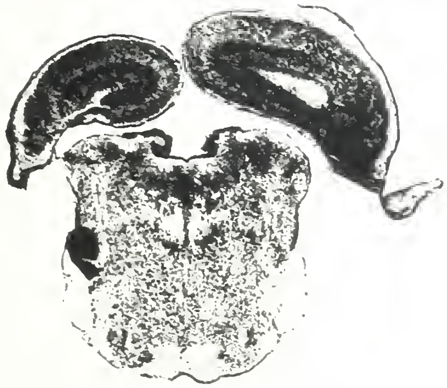

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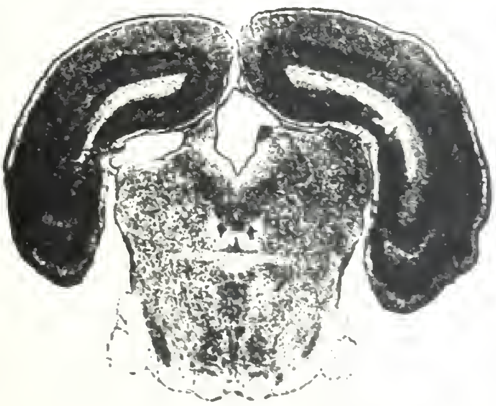

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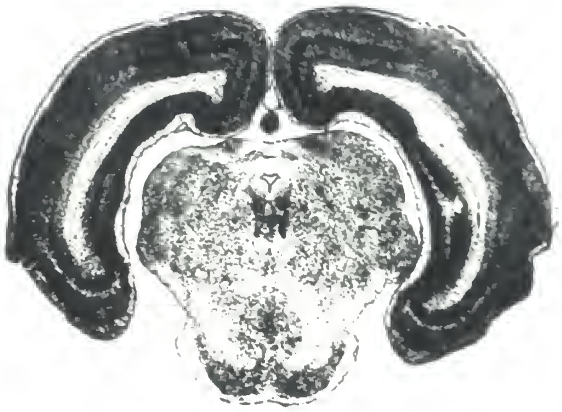

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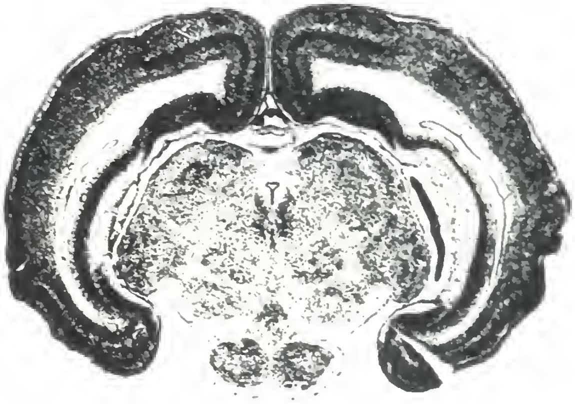

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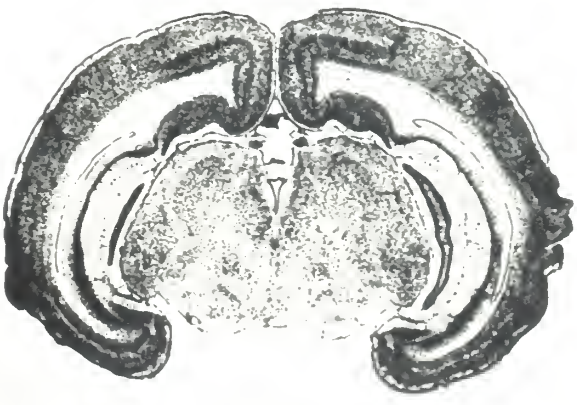

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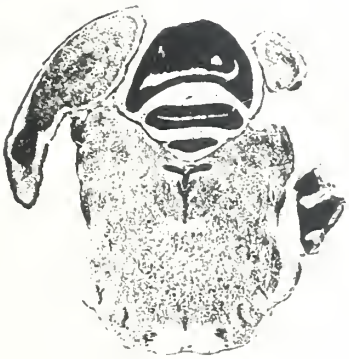
medial than the antero-lateral half of the superior colliculi. However, in contrast to Tupaia 309, the superficial layers of most of the anterior portions of both superior colliculi in animal 394 were removed; small pieces of layers 1 and 2 remained on the lateral edges on the right. This animal also received some damage to its inferior colliculus and central grey. The third animal, Tupaia 310, also had an incomplete but large lesion (see Figure 26). In this animal the lesion included most of both superior colliculi but spared the deeper layers anteriorally and both the deep and superficial layers laterally. Again in this case, portions of the inferior colliculus and central grey were included in the lesion. There was also slight damage to the pretectum.

Finally, three animals received unilateral lesions of the right superior colliculus (387, 388, 389). Tupaia 388 and 389 had lesions which were quite similar in extent (see Figure 27). In both cases, almost the entire right superior colliculus was removed except for portions of the deepest layers. In Tupaia 389 the left superior colliculus was also slightly damaged. The lesions of both of these animals also included almost the entire inferior colliculus and invaded both the central grey and tegmentum. The third animal, Tupaia 387, had a smaller lesion which spared anterior portions of the right superior colliculus and also left far more of the inferior colliculus and central grey intact. In all other respects, the lesion was similar to that of Tupaia 389.

Those animals which were selected for anterograde degeneration

Figure 26. Selected Cresyl Violet Stained Sections Through the Large but Incomplete Lesion of the Superior Colliculus in Tupaia 310. The lesion in this animal spared anterior and lateral portions of both superior colliculi, particularly the deeper layers. In addition to the superior colliculus, the lesion included some damage to the pretectum and central grey, particularly on the left. The cortex was not damaged in this animal; the small size of the cortex in Sections 28 and 30 is due to the uneven plane of cut.

TUPAIA 310



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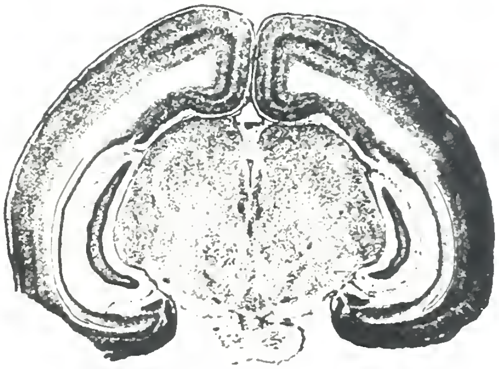

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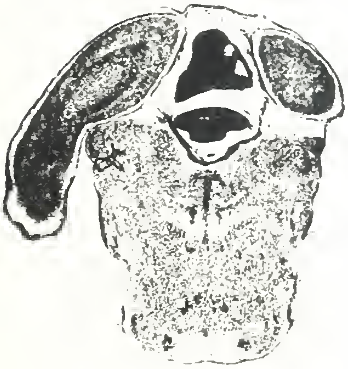

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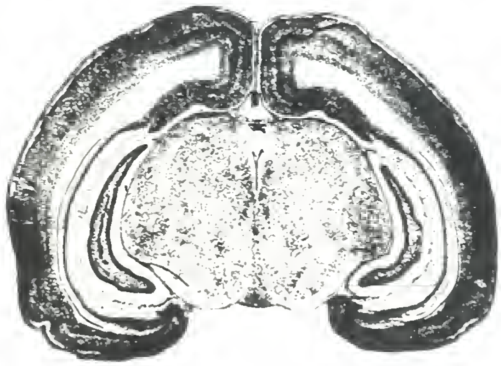

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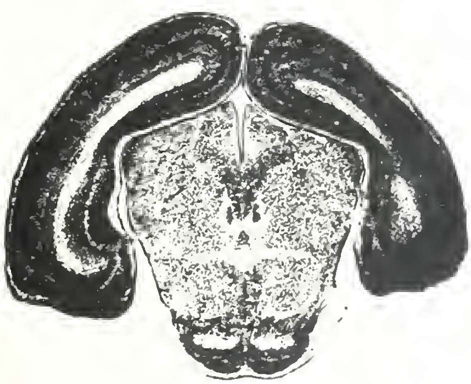

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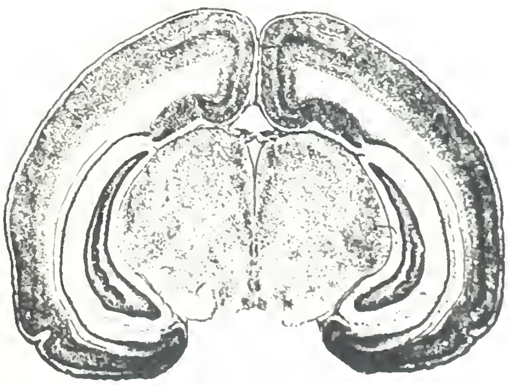

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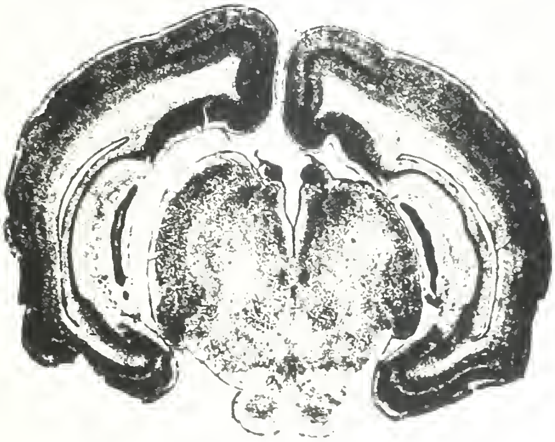
Figure 27. Selected Cresyl Violet Stained Sections Through the Unilateral Lesion of the Superior Colliculus in Tupaia 389. This lesion included almost the entire right superior colliculus with the exception of a portion of the deepest layers rostrally, the inferior colliculus, and portions of the central grey and tegmentum. There was also slight damage to the medial edge of the left superior colliculus.

TUPAIA 389



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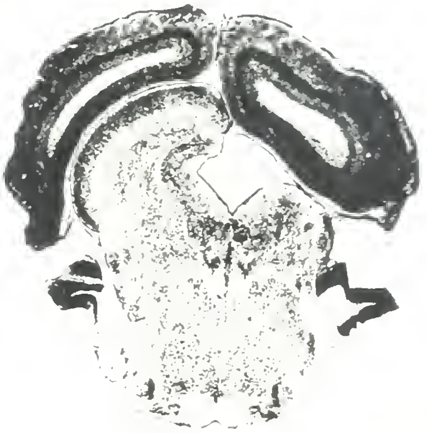

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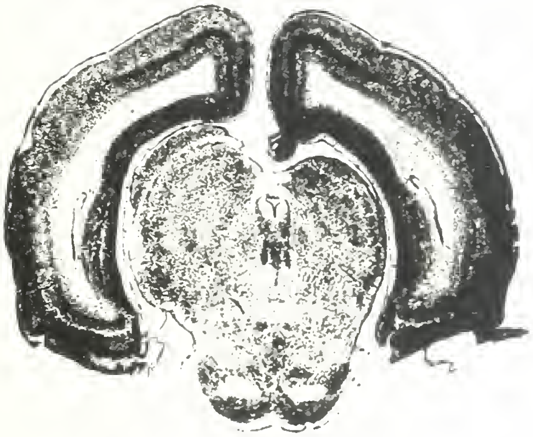

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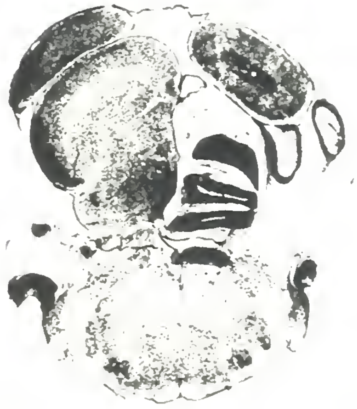

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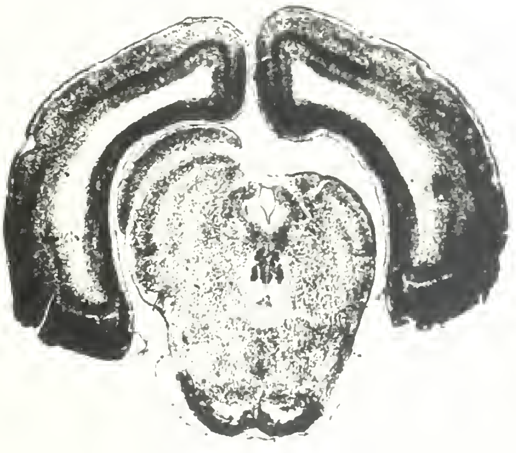

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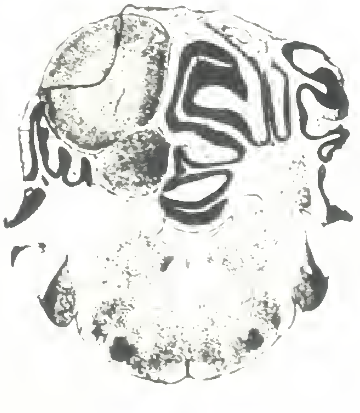

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analysis (see Method) showed similar changes in the distribution of their retinal fibers as was noted for animals following neonatal damage to the superior colliculus in Experiment I. These changes included the development of an anomalous retinal projection to the pulvinar nucleus and a slight increase in the density of input to whatever remained of the pretectum. Also, in all animals with damage to the superior colliculus in infancy, the cells of the pulvinar nucleus showed signs of degenerative changes.

Conclusions

The behavioral observations of Experiment I showed that the effect of the lesion of the superior colliculus was dependent upon the depth of that lesion. Those animals with superficial lesions appeared normal on tests of visual guidance, while those animals with deeper lesions appeared blind or grossly impaired. These results were confirmed by the more rigorous perimetry tests conducted in the present experiment. The present experiment added further details concerning the nature of the deficit following the larger lesion. First, it was found that, if a lesion spared a portion of the colliculus, the animal could orient to and follow stimuli in that part of the field which would be represented on the spared portion of the colliculus (see Lane et al., 1971). Second, it was found that animals with very extensive lesions were also poor at locating auditory and somatosensory stimuli, although they could localize prolonged

painful stimuli. Third, if the pretectum was sufficiently damaged, the animals showed defective pupillary responses, although all animals regardless of lesion could move their eyes. Finally, it was shown that animals even with very large lesions could run through and around a set of barriers better than would have been predicted by their scores in the perimetry tests, suggesting that in certain circumstances these animals did have the capacity to guide visually.

DISCUSSION

The main results of these experiments have shown a difference in symptoms depending upon the depth of the lesion of the superior colliculus. It is tempting to suggest that there are two syndromes rather than one complete and one partial or incomplete syndrome, because the animals with superficial lesions had severe deficits in the ability to distinguish the orientation of triangles and disturbances in color discrimination without concomitant defects in visual guidance which appeared following the deeper lesions. Therefore, while a double dissociation was *not* achieved, one might expect that it could be achieved if the deeper lesion was made without damage to the superficial laminae. One way to test this expectation would be to cut the efferents from the deeper laminae, and this experiment is now in progress with encouraging results.

Anatomical studies of the connections of the superior colliculus in the tree shrew lend support to the idea that there are two divisions. The superficial laminae have been shown to receive fibers from visual centers, the retina and visual cortex (Abplanalp, 1970; Campbell, Jane, & Yashon, 1967; Glickstein, 1967; Harting & Noback, 1971; Laemle, 1968; Tigges, 1966). In turn, they send efferents to the pulvinar and dorsal

lateral geniculate nucleus from which information can be relayed back to both striate and extrastriate visual cortex, respectively. Efferents are also projected from these layers to the pretectum and ventral lateral geniculate nucleus. In contrast, the deeper laminae receive multimodal input and send a major projection to motor areas of the brainstem and thalamic areas not usually associated with vision, such as the posterior nucleus, the intralaminar complex, and regions of the subthalamus (Casagrande et al., 1972; Harting et al., 1973; Martin & Harting, 1972). The difference in connections between the superficial and deep laminae is exactly what one would predict if the superficial layers were more involved in visual perception while the deeper layers were more closely tied to mechanisms controlling orientation of the head and eyes to sensory stimuli.

The connections just described, while helpful in explaining the main behavioral findings in the present experiment, pose a puzzle for the interpretation of these same results. If the animals with superficial lesions were normal in their ability to orient visually, then how did the deeper layers receive the visual information necessary to maintain the behavior? One possible source is suggested by an earlier finding of Schneider (1970). He speculated that the recovery of the ability to orient and track objects following superficial lesions in neonatal hamsters could be attributed to aberrant retinal fibers growing into the deeper layers. However, no such pathway was seen in the tree shrew. Another

possible source could be whatever remained of the superficial layers, since the superficial lesions in the present experiment did not totally remove all three superficial laminae. Therefore, it is possible that these remaining pieces supplied the necessary visual information to the deeper layers.

A number of other possible sources of input to the deeper layers also exist, for example, the ventral lateral geniculate nucleus, the extrastriate visual cortex, and the frontal eye fields of the cortex. If it is correct that the deeper layers are not dependent entirely on the superficial layers, as the present experiment suggests, then a number of implications follow which could provide the starting point for further experiments. One way that one might test whether the deeper laminae could function "normally" in the absence of direct retinal input would be to split the optic chiasma, since there is evidence that the retinal input to the superior colliculus in the tree shrew is completely crossed (Tigges, 1966). Such a preparation would have remaining to it all ipsilateral visual information going to the other visual areas, and this information could in turn be projected back to the superior colliculus. One could achieve part of the same result by removing, say, the right eye and right superior colliculus. In that case, the left superior colliculus would receive no direct retinal information but could receive visual information via other routes as described. Preliminary tests of visual tracking and orientation, as described in Experiment II, have been performed

on two animals with removal of the right eye and right superior colliculus. These animals exhibited brisk orienting responses close to the midline but appeared unable to visually follow a moving target. Assuming that the lesions were complete (histology is not yet available), at least some visual information important to visual guidance can reach the superior colliculus by routes other than via a direct route from the retina.

Nature of the deficit

If there are in fact two syndromes associated with two subdivisions of the superior colliculus, then the question which remains is how should each be characterized? For example, would it be fair to call the superficial syndrome a loss of pattern perception and the deeper syndrome a loss of the ability to orient the head to a stimulus? Clearly, neither statement appears adequate to describe the combination of symptoms which occurs after either superficial or deeper lesions. Following damage to the superficial layers, the animals were not able to distinguish the orientation of triangles and had difficulty in distinguishing certain chromatic from achromatic stimuli, yet they could distinguish light from dark, a pattern based on the orientation of stripes, and two chromatic stimuli from each other. Therefore, the superficial layers of the superior colliculus do participate in particular types of pattern or color discriminations but are not essential for all such discriminations. It is not as yet clear how the superior colliculus participates in these discriminations. A clue may be provided by comparing the deficits following

damage to the superficial superior colliculus with damage to other parts of the visual system in the tree shrew. When damage is restricted to the striate cortex, tree shrews have no trouble with any of the discriminations described above (Killackey et al., 1971; Snyder & Diamond, 1968; Snyder et al., 1969). However, when damage is restricted to the extrastriate visual cortex (an area which receives indirect input from the superior colliculus via the pulvinar nucleus), then the tree shrews, like those with collicular damage, have trouble discriminating triangles, yet no trouble discriminating stripes (Killackey et al., 1971). Further studies of deficits following damage to the extrastriate visual cortex have suggested that this area plays a role in "shifting attention" (Killackey, Wilson, & Diamond, 1972). It is possible that the superficial layers of the superior colliculus are organized to aid in certain aspects of attentional shift as defined by these experiments. Such a mechanism may be important when an animal is required to analyze a complex stimulus such as the orientation of a triangle located in a small part of the field. In the case of the discrimination of the orientation of stripes, an animal is not faced with such a difficult task since no matter where his attention is focused upon the stimulus card the relevant information is always present.

Presumably, the superficial layers of the tree shrew superior colliculus also relay information concerning the form of the stimulus, since without striate cortex tree shrews are easily able to discriminate

simple patterns and colors (Killackey et al., 1971; Snyder & Diamond, 1968; Snyder et al., 1969). It is doubtful that the superior colliculus by itself is capable of sustaining anything except rudimentary pattern vision, since larger lesions which include both striate and extrastriate cortex disrupt pattern discrimination (Snyder & Diamond, 1968). Apparently the information must first reach either the pulvinar or the extrastriate visual cortex before it becomes meaningful. The situation with color perception appears to be slightly different. Curiously, even after very large lesions which heavily damage both striate and extrastriate cortex, tree shrews still showed good color perception (Snyder et al., 1969). Furthermore, the present study clearly demonstrated that the superior colliculus of the tree shrew is important in color perception: all animals with lesions (superficial or deep) had difficulty on several of the color discrimination problems. Nevertheless, the superior colliculus did not appear to be essential for color perception, since all but one animal with complete removal of the superior colliculus were eventually able to discriminate blue from red when intensity was randomly varied. Why the superior colliculus and not the striate cortex is more important in the perception of color in the tree shrew is not clear. It also remains to be proved whether this information must be relayed to the extrastriate cortex before it is meaningful, since in the investigations of Snyder and Diamond (1968) none of the lesions included all of the pulvinar projection area.

Characterizing the nature of the syndrome following the deeper superior colliculus lesions is complicated by the fact that these lesions always included the superficial layers and, presumably for this reason, the animals also showed similar losses in visual discrimination. Let us consider that portion of the syndrome which was unique to the deeper lesions. The animals with deeper lesions, particularly those with the largest, most complete lesions, can best be characterized by their appearance of blindness. This appearance of blindness following total removal of the superior colliculus in the tree shrew confirms an earlier report (Jane, Levey, & Carlson, 1972). Behavioral observations described in Experiment I showed that these animals were unresponsive to visual threat and appeared to neglect both small stationary and moving stimuli yet did not run into objects in their path. Attempts to quantify this deficit in Experiment II confirmed these results and, in addition, showed that animals with incomplete lesions recovered the ability to orient to or follow objects in those parts of the visual field which would be represented on the intact tissue (see Lane et al., 1971). Furthermore, with two exceptions Experiment II showed that the animals with total removal of the superior colliculus were unable to orient to and follow objects presented in any part of the field. However, two animals with what appeared to be nearly complete lesions did show a surprising ability to orient to objects within 30° of the midline or within the area of binocular overlap for the tree shrew. It is not clear whether this ability was due to the few

remaining cells in the tectum[1] or to adjacent structures such as the pretectum and central grey. In all cases where the animals showed no response, the pretectum and central grey were severely damaged.

From these observations it was clear that deep lesions of the superior colliculus of the tree shrew in some way disrupted mechanisms which directed the animal's head toward a stimulus and kept it within view as it moved. This deficit was not exclusively a visual deficit, since the animals also showed similar though less severe losses in the ability to locate auditory and somatosensory stimuli. The animals were not "blind" in the strict sense, since the animals did show their awareness of visual stimuli in other ways. They could discriminate horizontal from vertical stripes (Experiment I) and were able to orient to and move through openings in a set of serially arranged barriers (Experiment II). Also, though they did not orient well to sound or touch, they did show their awareness by an increased frequency of "freezing" or escape responses. The deficit was also not strictly motor since they could easily use their neck muscles to turn their heads while grooming. Furthermore, the neurological tests and the tests with the barriers (Experiment II) suggested that the inability to orient to, or the inattention to visual stimuli, was specific to certain situations. If a small stimulus was presented to the animal, it was

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[1] One of the difficulties with ablation studies of the superior colliculus is in the definition of the boundaries (particularly deep) of the superior colliculus (for discussion of this point, see Berlucci, Sprague, Levy, & Di Berandino, 1972).

ignored. If, however, the same animal was in motion, that animal appeared to be able to orient himself rather well to an opening in a barrier and to avoid obstacles in its path. Possibly, in the second situation--that is, while the animal moved itself--visual information about object position was picked up which was either not available or neglected in the first situation. The sizes of the objects (a small worm versus a large doorway in a barrier) may also have played a role in the animal's success or failure following its lesion. Numerous further tests would be necessary before one would want to do more than simply speculate about these differences.

Comparison with other studies: similarities

The present experiments have shown that in the tree shrew the superior colliculus contributes information which is important both to the identification and location of objects and, further, that the colliculus itself may be functionally subdivided with respect to its contributions to each type of information. The question which now remains to be answered is whether the organization and function of the superior colliculus is unique to the tree shrew or whether it shares features in common with other species.

Studies of the superior colliculus in other mammals suggest that there may be some common trends. In the hamster, undercutting the colliculi has been shown to cause permanent losses in visual and acoustic

localization and transient losses of tactual localization (Schneider, 1968, 1969). In fact, Schneider used the term "tectal blindness" to describe such hamsters, since they behaved initially as if they were blind, much like the tree shrews in the present study. The hamsters, however, were not blind in the true sense, since they were able to distinguish horizontal from vertical stripes. In contrast, hamsters,following removal of the visual cortex, were unable to distinguish the orientation of stripes but were able to localize visual and auditory stimuli. From these results, Schneider concluded that the visual cortex was concerned with object identification, while the superior colliculus was concerned with the location of objects and probably did not play a role in visual discrimination. Yet, in a second investigation Schneider (1970) was able to demonstrate that hamsters which underwent complete striate ablations as neonates and subsequently had their superior colliculi undercut as adults were still able to discriminate horizontal from vertical stripes, although they were unable to orient appropriately. Schneider suggested that this preservation of pattern vision may have been the result of a lack of damage to the collicular pathways to the thalamus (all of his lesions were made by undercutting the colliculi from a posterior approach). This result fits well with the present notions of the organization of the superior colliculus in the tree shrew, particularly with respect to the idea that there may be two functional subdivisions.

In the cat, like the hamster, total bilateral removal of the superior

colliculus in neonates or adults has been shown to cause neglect and poor localization of visual, acoustic, and somatosensory stimuli (Norton, 1971; Sprague & Meikle, 1965). Moreover, such lesions in cats have been shown to result in deficits in pattern recognition (horizontal versus vertical bar; upright versus inverted triangle; cross versus circle), although such deficits were specific to original learning and not to retention (Berlucchi et al., 1972; Sprague et al., 1970). No effort has been made to determine if such deficits could be reproduced if damage were restricted to the superficial layers of the superior colliculus in the cat. However, there is at least partial evidence that some of the deficits associated with total colliculus removal in the cat are separable neurologically. Voneida (1970) found that following a midline lesion of the brainstem tegmentum (such a lesion would interrupt one of the major descending pathways from the tectum, the predorsal bundle) animals were unresponsive to visual threat although they easily learned to discriminate between a cross and triangle and were able to navigate through doorways in barriers. It is noteworthy that this lesion in the cat reproduced a part of the syndrome seen after large deep lesions of the superior colliculus in tree shrews without producing any deficit in visual discrimination, suggesting the existence of a functional subdivision.

Several electrophysiological and anatomical studies also support the notion that there may be a division of labor between upper and lower laminae of the cat colliculus. Straschill and Hoffman (1969) found that

the majority of cells in the superficial laminae had small, well-defined visual receptive fields which responded either to static or moving stimuli. According to Graybiel (1972), these superficial cells send their information principally to visual areas of the thalamus, while cells in the deeper layers send major projections to brainstem motor areas in a manner similar to that described above for the tree shrew. Single unit investigations of cells in the deeper laminae of the cat suggest that, in contrast to the cells in the superficial layers, these cells respond best to visual or auditory (sometimes also tactile) stimuli moving in a particular direction (Sterling & Wickelgren, 1969; Straschill & Hoffman, 1969; Wickelgren, 1971). Schaefer (1970) has hypothesized that these multimodal units may serve as part of a mechanism by which eyes and ears are directed toward a stimulus source. Presumably, cells with comparable properties also exist in the superior colliculus of the tree shrew since both cat and tree shrew show losses in visual, auditory, and tactile localization after collicular ablation.

Comparison with other studies: differences

From the above discussion, it can be concluded that the functional organization of the tree shrew superior colliculus is probably not unique but shares features in common with at least two species belonging to separate mammalian orders, the cat and the hamster. However, some caution must be exercised in drawing such parallels since studies of the

Cats can orient in

superior colliculus in these and other species (in particular, the monkey) point to some important differences. For example, no deficits in pattern or color perception were found in the rhesus monkey with up to 80% destruction of the superior colliculus (Anderson & Symmes, 1969; Rosvold, Mishkin, & Szwarzbart, 1958). If, however, these lesions included damage to the posterior thalamus and pretectum, mild deficits in discrimination learning were found in some animals (Anderson & Symmes, 1969). Involvement of the pretectum in the cat appears to exaggerate the discrimination deficits which are found after collicular ablation (Berlucchi et al., 1972). By contrast, evidence from the present experiments suggests that in the tree shrew the pretectum is not involved in the visual discrimination deficits seen after superficial collicular ablation, although it may contribute to the syndrome seen after deeper lesions.

With respect to visual guidance, it appears to be the case that only tree shrews and hamsters suffer the permanent losses which can best be referred to as "tectal blindness." After colliculectomy, cats eventually are able to orient to visual stimuli in the binocular area of the visual field (Sprague & Meikle, 1965). In the rhesus monkey, damage to the superior colliculus, including the deepest layers, causes only minimal and transient deficits in eye movements, visual following, and visual orientation (Anderson & Symmes, 1967; Pasik, Pasik, & Bender, 1966; Wurtz & Goldberg, 1972). Again, only when the lesions included heavy invasion of the pretectum and central grey did monkeys show visual

neglect and deficits in visual guidance which were in any way comparable to those seen in the tree shrews in the present experiments. Damage to the pretectum in the monkey, with some concomitant damage to neighboring structures, has also been shown to produce deficits in visual guidance (Pasik, Pasik, & Bender, 1969).

It is curious that monkeys suffer no permanent deficits in eye movements, particularly in light of older notions concerning the importance of the superior colliculus for reflex eye movements. Primates and cats appear to rely more on eye movements for visual localization than either the hamster or the tree shrew, which tend to make more head movements for visual localization. Yet, hamsters and tree shrews suffer far more from damage to the superior colliculus than do monkeys. Wurtz and Goldberg (1972) have suggested that in the monkey the superior colliculus is not involved directly in moving the eyes but rather serves an "attentional" function, acting to facilitate in the orientation of head and eyes to an area of interest to the animal.

The same may hold true for tree shrews and hamsters. Moreover, these animals, with their laterally placed eyes and consequent wide visual fields, may depend more heavily on the superior colliculus in order to be alert to the approach of predators and, in the case of tree shrews, perhaps also to localize and identify potential prey rapidly.

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